Braided river springs: distribution, benthic ecology, and role in the landscape

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Abstract

Alluvial springs are an interesting feature of braided river flood plains. The aim of this study was to quantify and characterise the fauna and physicochemistry of these springs. The distribution and occurrence of springs was assessed using a GIS analysis in 20 South Island braided rivers. The greatest number of springs was found in east coast inter-montane valleys, 65% of which were associated with obstructions in the river valley, such as alluvial fans, bluffs or flood retention works. A comparison between springs, hill slope streams and main channels in the upper Waimakariri River revealed physically disparate environments, which were reflected by their invertebrate communities. Springs contained the greatest number of unique taxa, which was attributed to high stability and the presence of phreatic taxa. In spring-sources the presence of aquatic plants were found to be a powerful structuring influence on benthic invertebrate communities. The generalist, asynchronous nature of New Zealand benthic invertebrate fauna, and the high diversity and evenness of predatory taxa are also thought to be influential on the high levels of taxonomic richness at spring-sources. Away from the spring-source taxonomic richness decreased due to the decline in stability and habitat complexity. Spring age, or time since major disturbance, was important in structuring benthic invertebrate communities. Older springs were dominated by non-insect taxa, whereas younger springs, were dominated by insects which are rapid dispersers. A macrophyte manipulation experiment was conducted in four spring-sources. The removal of macrophytes from treatment plots resulted in a decrease in taxa abundance, but an increase in evenness. Mayflies and caddisflies increased, replacing mollusca and diptera. This shift in community

composition may have been due to changes in available living space, food resources, flow characteristics and physical structure between the cobble and macrophyte habitats. Springs contributed a major proportion of the benthic invertebrate biodiversity to the upper Waimakariri River and this study confirms that they deserve commensurate consideration in regional river management planning.

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Chapter 3: the contribution of springs to river corridor bio-diversity

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A review of cold water spring ecology: with particular emphasis upon alluvial flood plain springs

Photos: Duncan Gray

1.1 Introduction and terminology

Springs are unique habitats in the realm of running waters. A spring is a natural outflow of groundwater that may create a lotic, lentic or wetland environment. These habitats differ markedly from surface and rain water fed systems because of the relative constancy of groundwater discharge and physico-chemical conditions. As such, and due to the relatively limited number and distribution of springs, they support a variety of relatively rare and unusual fauna (Percival 1945, Glazier 1991, Di Sabatino et al. 2003). Springs are a common feature of many alluvial flood plains and consequently play an important role in the ecology of the alluvial riverine landscape (Stanford 1998, Arscott et al. 2000, Burgherr et al. 2002, Ward et al. 2002). They provide refuges from disturbance events, a source of colonists post event and a permeable ecotone for the interaction of phreatic and surface communities (Stanford and Ward 1988).

1.1.1 Types of springs

Cold, freshwater springs resulting from natural surface up-welling of groundwater, form a unique array of habitats within their specific geomorphological, climatic and ecological context. In New Zealand there exists a wide diversity of springs, from tiny seepages to one of the worlds largest cold water springs at Waikoropupu (averaging $11m^3/s$) (Michaelis 1974). Any point at which groundwater reaches the surface can be termed a spring, however a number of specific types have been defined. In limestone, or karst areas springs may be described as re- or ex-surgence (www.speleogenesis.info/index.php 09:00 22.03.2005). A re-surgence is the resurfacing of an underground stream that has an upstream surface component.

Waikoropupu Springs is an example of a re-surgence, the waters being derived predominantly from the Takaka River some 15 km from the springs and flowing through fissures in the Arthur Marble before returning to the surface. An ex-surgence is an emerging stream whose headwaters are unknown, although an approximate surface catchment can be surmised. The sources of the Pearce and Riwaka Rivers in Nelson are examples of ex-surgences. The difference between karst springs and an alluvial spring is in the passage of water through the aquifer. Faulting in karst bedrocks permits a discrete flow of water, an underground stream, whereas alluvial groundwater must percolate diffusively through interstitial spaces, such that any variation in local precipitation is homogenised by the greater aquifer. However, for the purposes of this review the term spring will be used to encompass all groundwater emergence systems, with attention being drawn to different aquifer types when appropriate.

Springs have been classified, variously according to their hydrogeology, physico-chemistry, fauna and source characteristics (Zollhoefer et al. 2000). However, few classifications have encompassed an ecological perspective in trying to characterise discrete spring types. Classifications based on hydro-geological parameters incorporate the aquifer type or bedrock structure, which channels ground-water flow to the surface. Hydro-geology types can distinguish between, for instance, depositional characteristics of aquifer sediments (Hoffsten and Malmqvist 2000) and faulting in karst bedrocks (Smith et al. 2003). Physico-chemical classifications consider the prevalent, defining characteristics of water at the spring source, such as temperature in thermal (Hayford and Herrman 1998), cold (Erman 1998) and variable (Smith et al. 2003) springs.

The use of macro-invertebrate fauna as indicators of prevailing in-stream conditions (Stark 1998, Boulton 1999, Joy and Death 2003) has also been applied to the classification of springs (Glazier 1991). The majority of recent studies have combined faunistic data with a suite of physico-chemical and hydro-geological characteristics to not only classify springs, but examine the forces driving the structure of macro-invertebrate communities (Vanderkamp 1995, Webb et al. 1998, Hoffsten and Malmqvist 2000, Zollhoefer et al. 2000). However, due to the local specificity of faunistic records and the inherent complexity of any multivariate classification few contemporary classifications have become widely accepted. The most universally accepted classification is that proposed by Steinman (1915) and modified by Theineman (1924) which, proposed the terms rheocrene, limnocrene, and helocrene. The rheocrene, or gushing spring, discharges directly into a stream channel, often forming a distinct stream source; limnocrenes in contrast have lentic headwaters, discharging into pools, which may or may not possess an outflowing, rheocrenal stream. Finally, helocrenes are characterised by diffuse up-welling over boggy or marshy ground (Lindegaard 1998). This classification of Steinman's has endured probably due to its simplicity, however the three classes are frequently subdivided using a further descriptor, such as a thermal rheocrene (Hayford and Herrman 1998) or an alluvial rheocrene (Zollhoefer et al. 2000).

Most braided river springs arise in the scoured out beds of abandoned braid channels and constitute alluvial rheocrenes. Generally, these streams have a distinct source, however occasionally ponding may occur to form limnocrene habitats. Any classification of braided river springs is confounded by the scale at which the springs

are viewed. Although each discrete spring source can be defined as a rheocrene or limnocrene, springs maybe clustered within a complex diffuse wetland (Johnson and Gerbeaux 2004), which fits the definition of a helocrene according to Lindegaard (1998).

1.1.2 Zones within springs

Longitudinal changes along stream channels have long been recognised as important for the regulation of physical and biological conditions (Vannote et al. 1980, Winterbourn et al. 1981). Downstream changes within spring-fed streams occur rapidly, depending on the relative degree of groundwater influence. The physicochemically stable conditions close to the spring source gradually become more variable and more reminiscent of a rain-fed stream (McCabe 1998). These patterns of physicochemical fluctuation, particularly thermal constancy, have been used to delineate between the spring-source and the spring brook. The downstream boundary of the eucrenal zone is marked by the point at which annual temperature variation becomes >2ºC, whereas stream habitat below this point is designated hypocrenal (Smith et al. 2003) (Figure 1).

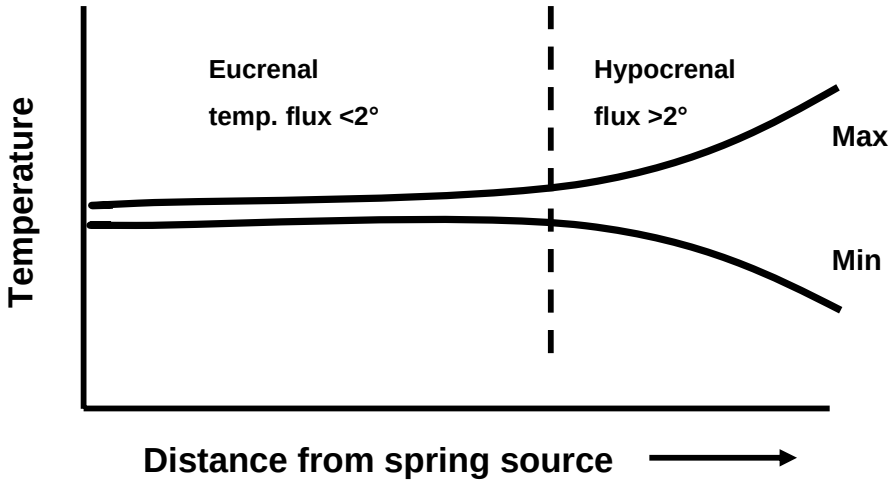

Figure 1. Schematic diagram showing the magnitude of temperature variation with increasing distance from spring-source. The boundary between the eucrenal and hypocrenal zones is the point at which temperature varies by more than 2°. This transition is unlikely to be stable over time due to the input of surface-water during precipitation and fluctuations in groundwater discharge dictated by local aquifer stage height.

1.1.3 Faunal groups

Other classifications have been produced to group fauna according to their occurrence in springs (Lindegaard 1998). For example, crenobiontic species are those that live entirely in springs, predominantly within the eucrenal zone. Taxa may include organisms which preferentially inhabit groundwater systems and are present in the eucrenal as a result of "overflow" from the aquifer. An example includes the New Zealand amphipod *Paraleptamphopus subterraneus* (Death et al. 2004). Alternatively Crenobiontic taxa may be glacial relicts using springs as thermal refugia and are restricted to the ecotones around the point of groundwater up-welling (Nielsen 1950, Michaelis 1974, Sykora and Weaver 1978). Crenophilous species reach their maximum density in springs, but penetrate downstream into the hypocrenal zone. In New Zealand cased caddis larvae from the genus *Zelolessica* are common in streams emerging from springs, and are frequently found within the dense bryophyte and macrophyte beds that occur due to the high levels of flow and substrate stability (Death et al. 2004). Many lotic species, which occur across the spectrum of flowing

waters, are also found in springs. For example, the leptophlebiid mayfly *Deleatidium* spp. can be found in most aquatic habitats, including springs, although it reaches its highest densities in disturbed gravel bed rivers (Sagar 1983, Scrimgeour 1987). Similarly, numerous lentic species can be found in ponded or limnocrene springs but rarely reach their maximum densities at such sites. Lindegaard (1998) also describes madicolous species which inhabit thin water films around seepages and waterfalls. A further addition to these groups is the ephemeral spring dweller, a species which is found in temporary groundwater fed pools. Ephemeral spring dwellers may also appear in rain-fed temporary pools, but their highest densities are in groundwater fed habitats that have reduced physico-chemical fluctuations, and more prolonged periods of wetness. For example, the diving beetle *Huxelhydrus syntheticus* Sharp is known only from shallow temporary pools, on the beds of braided rivers east of the Southern Alps (Winterbourn et al. 2000).

1.2 The physical environment of springs

1.2.1 Aquifer types

The physical environment of a spring is determined by its geomorphological setting. The aquifer and emergent surface terrain dictate discharge, temperature, water chemistry, dissolved oxygen concentration, substrate, habitat permanence and organic matter levels (McCabe 1998, Hoffsten and Malmqvist 2000, Smith and Wood 2002). Some of the most obviously different spring types are those that drain deposits of erosional material, (e.g. flood plains or scree slopes), and those that exist within fault and cave systems, commonly associated with karst landscapes. Karst springs can be considered as intermediate between surface-water-fed streams and alluvial springs, as they often exhibit fluctuating discharge and temperature, and high organic matter

levels (McCabe 1998). Physicochemical variation in karst springs is dependent upon the depth, size and stability of the aquifer that feeds them.

Aquifers contained within eroded materials can be further divided by their emergent terrain and size. Permeable hill slopes and rubble filled gullies on mountain sides often contain steep, shallow, fast-draining aquifers. In these systems a change in slope or the presence of impermeable bedrock may cause water to return to the surface as springs, which are often the source of mountain streams (Johnson and Gerbeaux 2004). Because of their small size and small catchment area these springs may be ephemeral and react quite strongly to localised precipitation. In contrast, larger aquifers occur beneath lower gradient flood plains of rivers.

Flood plains usually occur well down the river continuum (stream order 3-6), in depositional zones where the accumulation of fluvial sediments creates extensive, relatively planar, valley floors containing the stream channel and aquifer (Woessner 2000). Gravel bed rivers with flood plains are common worldwide, especially in glaciated areas (Hey et al. 1982) and springs are commonly reported in these systems from the North America, Europe and New Zealand (Stanford and Ward 1993, Digby 1999, Arscott et al. 2000). The flood plain alluvium is saturated by laterally influent river water and by up-welling groundwater, forming an alluvial aquifer bounded either by bedrock or an impermeable sediment layer. The aquifers beneath such flood plains have a relatively gentle slope and consequently water velocities are low and residence times high. As large rivers drain large catchments spring discharges may have a more constant flow and be less responsive to local precipitation.

1.2.2 Flood plain springs

Flood plain alluvium is derived from riverine processes that are depositionally complex and exhibit relatively high permeability to water (Woessner 2000). Zones of variable permeability exist within alluvial aquifers, which correlate with 3-dimensional depositional structure of the flood plain e.g. old braid channels, which are orientated parallel to the direction of valley flow. These underground preferential flow channels, or paleochannels, create the high levels of hydrological connectivity now recognised as important interactive pathways between the river channel, riparian zone, aquifer and spring habitats (Stanford and Ward 1988, Ward et al. 2002). Paleochannels have been mapped using ground-penetrating radar and frequently can be identified from aerial photos (Figure 2) (Huggenberger et al. 1994, Huggenberger et al. 1998, Poole et al. 2002). Stanford and Ward (1993) suggested that paleochannels may be successive elevations of the laterally migrating river channel that became buried as alluvial deposits form the flood plain. Alternatively they may have been formed by intensive outwash periods during glacial retreats and buried by subsequent floods. Huggenberger et al. (1994) add that paleochannels may be areas of active channel that become uniformly filled during an aggradation event. Stanford and Ward (1993) describe a general pattern of down-welling main channel water at the head of a flood plain, augmented by lateral flow from hill slope sources, and then variable degrees of up-welling along the flood plain reach determined by the depth of impermeable sediments, intrusion of bedrock outcrops and encroaching canyon walls. Up-welling may occur within the river main channel or within the beds of abandoned braid channels across the flood plain. Recent research at the Flathead River, Montana has shown that a sinuous lattice of preferential flow paths exists at the same elevation as the main channel's stream bed. Consequently, changes in the elevation of the main

channel bed relative to flood plain elements, specifically the beds of abandoned braid channels, allow up-welling and the formation of springs at any point along a flood plain reach lower than the main channel bed (Poole et al. 2002). Any point on a flood plain surface lower than the main channel bed, therefore is likely to be characterised by up-welling ground-water. In extreme circumstances although surface-water in the main channel may dry up, substantial interstitial flow remains in the aquifer and spring habitats which are lower than the main channel (Gray pers.obs).

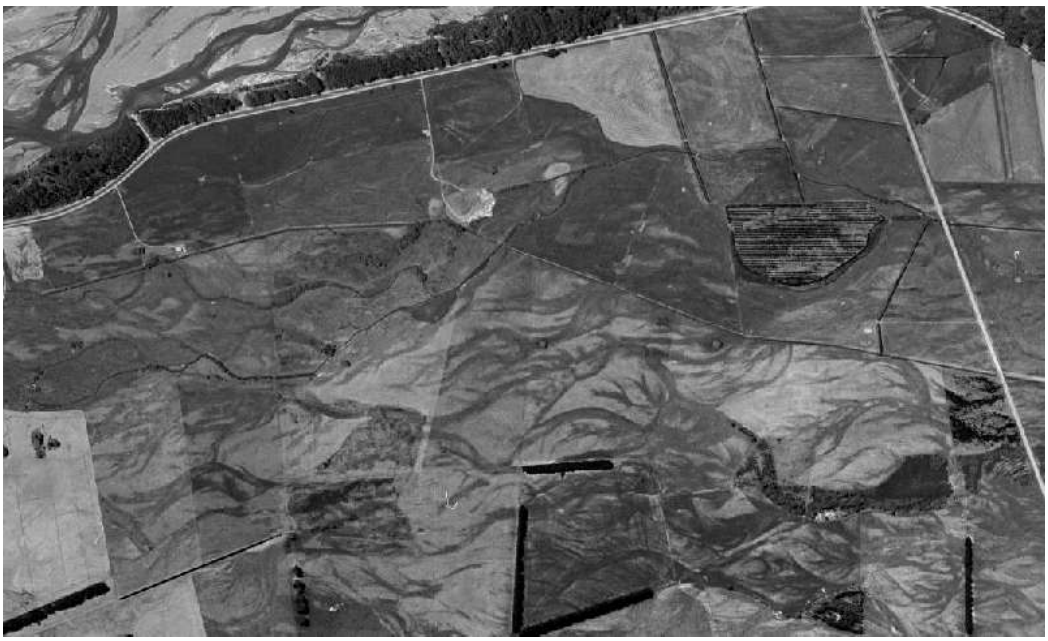

Figure 2. Section of the Waimakariri flood plain, north of Christchurch, showing numerous paleochannels or buried braid channels which provide zones of high permeability for aquifer water. Numerous springs arise in these channels which form the source of the Waimakariri south branch or Otukaikino Creek.

The alluvial aquifer beneath flood plain surfaces is an integral part of the dynamic riverine landscape. Within the context of flood plain geomorphology, the movement of water, nutrients and organic matter along groundwater flow paths regulates the physicochemical and biological characteristics within a mosaic of springs, spring creeks, wetlands and main channel habitats across the flood plain. These variable levels of hydrological connectivity produce a wide range of aquatic habitats and

consequently high levels of habitat and potential biological diversity (Begon et al. 1996).

1.2.3 Discharge

Because springs emerge from underground aquifers their discharge is generally buffered against the high and low flows that characterise rain-fed streams. An exception to this are springs found in karst regions (McCabe 1998). Water in karst systems tends to have a short residence time in the aquifer because it moves through large cracks in bedrock as opposed to filtering through interstitial spaces between sediments (Smith and Wood 2002). Consequently spring discharge reacts more rapidly to rainfall in the karst catchment, a phenomenon which can be seen in some of New Zealand's karst springs, e.g., the sources of Pearse and Riwaka rivers, Nelson (Death et al. 2004). Karst springs such as Waikoropupu Springs (Nelson), that are fed by more stable aquifers, fluctuate less however. In contrast to most karst springs, alluvial flood plain systems have aquifer hydrographs indicating a less responsive relationship between surface-water and ground-water levels. In the Flathead River, Montana, main channel hydrographs were marked by distinct peaks in discharge, whereas water level in the aquifer remained relatively stable (Stanford and Ward 1988). Springs arising from this flood plain aquifer would exhibit a discharge determined by the stage height of the local aquifer, not discharge within the main channel. However, spring discharge would follow seasonal patterns as determined by the mean flow of water through the valley hydro-system. Within both karst and alluvial systems there will be a range of variability and absolute discharges depending on the depth and stability of the source aquifer. This variability in flow, particularly

when it results in springs being ephemeral, has a profound impact upon spring communities (Smith and Wood 2002, Smith et al. 2003).

1.2.4 Temperature

The temperature regime within aquatic habitats is ecologically important because almost all biological activity is temperature dependent. Aquatic invertebrates respond to temperature on several levels. Individuals respond physiologically in terms of metabolic and activity rates, lifecycles may be plastic under different temperature regimes, and the abundance and distribution of invertebrates is affected by patterns in absolute temperature, diel and seasonal amplitudes and rates of change (Ward and Stanford 1982, Allan 1995). For example brachycentrid trichopterans have been shown to reduce their feeding rates at high temperatures (Gallepp 1977), and Lutz (1974) showed that damselflies required longer developmental periods at lower temperatures. Harding and Winterbourn (1993) showed that life history synchrony of a New Zealand mayfly was less pronounced in a thermally stable lake-fed stream than a nearby run-off fed stream. A survey of Andean stream invertebrates across an altitudinal gradient revealed a gradual replacement of species as the thermal tolerance of each was reached (Jacobsen 2004). In New Zealand, summer water temperatures in excess of 20^{o}C are thought to explain the absence or low abundance of temperature sensitive mayflies and stoneflies (Quinn and Hickey 1990a). Exclusion might be the result of both lethal and sub-lethal effects of temperature, but presumably if there are specific temperature requirements for some portion of the life cycle then, species will be excluded from certain habitats based on temperature alone or the competitive advantage it confers to other species (Nielsen 1950). Invertebrates inhabiting springs have been shown to respond to temperature gradients. Ward and Dufford (1979)

noted low species diversity at spring-sources which they attributed to the deleterious effects of thermal constancy on certain species. The presence of certain crenobiontic species within springs has been attributed to thermal regimes. For example, the trichopteran *Apatidea muliebris* MacLachlan, found in Danish springs (Nielsen 1950) and the New Zealand flatworm *Prorhynchus putealis* Haswell, which disintegrates rapidly if the temperature is raised (Percival 1945).

Deep ground-waters generally exhibit a stable temperature that approximates the mean annual surface air temperature of the region, whereas highly variable temperatures occur in rain- and surface-fed streams (Brunke and Gonser 1997). Thermally stable springs thus exhibit temperature gradients between high and low altitude, and high and low latitude. Aquifers with a short residence time such as those found in karst regions may demonstrate greater fluctuations of temperature as may those fed by shallow aquifers within flood plains (Smith et al. 2003). Groundwater passing through shallow alluvium may be heated by solar irradiance or percolating surface-water (Brunke and Gonser 1997, Ward et al. 1999a). But in general, at the point of up-welling alluvial springs are relatively cool in summer and warm in winter, with limited diel, and seasonal fluctuations (Brunke and Gonser 1997, Brown et al. 2003).

1.2.5 Water chemistry

The chemistry of spring water is determined primarily by the residence time of water in the aquifer, the reactivity of aquifer materials and the chemical status of influent surface-water (Freeze and Cherry 1979). Surface-water fed streams exhibit considerable fluxes in solute concentrations. Groundwater, despite the variable

hydrochemistry of influent sources, tends to equilibrate with respect to solute concentration after extended contact with mineral substrate (McCabe 1998). Ionic enrichment and specific conductivity at spring sources therefore is often stable, but relatively high compared to that of surface-fed streams (Brown et al. 2003). Groundwater within the alluvial aquifer of the Flathead River showed a gradient of increasing conductivity with declining influence of main channel water, presumably due to its longer residence time and lower levels of dilution by low conductivity river water. A similar pattern of stable and enriched conductivity has been reported in both alpine streams (Milner and Petts 1994) and large, alluvial, flood plain springs (Stanford and Ward 1993). General patterns in the levels of specific ions are very complex and can only be described within the context of a specific system. Climate, flood plain morphology and alluvial reactivity, riparian vegetation, surface and subsurface biological communities combine through hydrological connectivity to regulate the levels of ions that occur at points of groundwater up-welling. Reviews of nutrient dynamics, nitrogen and phosphorus biogeochemistry at surface-subsurface ecotones, and the roles of riparian zones in stream and groundwater chemistry address these topics in great detail and are applicable to conditions found in spring habitats (Dahm et al. 1998, Duff and Triska 2000, Hendricks and White 2000) .

1.2.6 Dissolved oxygen

Dissolved oxygen concentrations are often low in up-welling ground-water (McCabe 1998, Craft et al. 2002). However, due to rapid re-aeration, spring water generally regains full saturation quickly (Lindegaard 1998). The amount of oxygen depletion in spring water is dictated by conditions along flow paths within the aquifer. Usually there is no production of oxygen in ground-water, therefore the oxygen status at the

point of up-welling is a balance between rates of transport from the atmosphere and rates of consumption below the surface. Variability in sediment composition and structure, groundwater flow velocity, organic matter content and the abundance and activity of micro-organisms, all affect oxygen levels along groundwater flow paths (Malard and Hervant 1999). Patterns are highly variable due to the further compounding effects of seasonal variation in aquifer recharge. Although it is likely that many spring sources do exhibit depleted oxygen concentrations, no evidence is available as to its effect upon invertebrate communities, nevertheless we might expect negative effects in some taxa (McCabe 1998) .

A common characteristic of springs is the presence of abundant macrophytes. High macrophyte biomass develops in the absence of substrate-disturbing flows (Sherwood et al. 2000, Riis and Biggs 2001), and has been linked to large diel fluctuations in oxygen concentrations due to the contrasting effects of photosynthetic and respiratory activity. Kaenal et al. (2000) investigated the effects of reach scale macrophyte removal in two high nutrient, low gradient, lowland streams in Switzerland. After macrophyte removal they recorded a reduction in diel oxygen fluctuation. Macrophyte respiratory intake of oxygen at night resulted in oxygen concentrations as low as 6 mg/l, approaching lethal levels for fish such as trout (< 5 mg/l) (Brooker et al. 1977). Thus, in spring habitats the deleterious effects of low oxygen concentrations in up-welling groundwater might be exacerbated during darkness by the respiratory activity of macrophyte beds.

1.2.7 Macrophytes and bryophytes

Constancy of flow and temperature regimes within springs is conducive to the formation of thick and diverse beds of macrophytes and bryophytes (Death et al. 2004). Sherwood et al. (2000) identified 23 species of macrophyte and three species of bryophyte along the 2 km length of a spring-fed stream in Ontario, and Michaelis (1974) recorded five angiosperm and ten bryophyte species in Waikoropupu Springs near Nelson, New Zealand, were they covered 54% and 28% of the spring bed respectively. In the Frankenwald, North-eastern Bavaria, Bierkuhnlein (1998) classified 23 springs according to macrophyte assemblages which were correlated with physicochemical conditions.

The presence of macrophytes and bryophytes in running waters have been linked to patterns in invertebrate communities (Humphries 1996, Death 2000). In New Zealand benthic invertebrates associated with macrophyte communities are dominated by molluscs, chironomids, crustaceans, amphipods and Trichopterans. Abundance is frequently high, but diversity is often low compared to that on rocky substrata (Death 1991). Evidence that assemblages differ between individual species of higher plant is equivocal, although Death (1991) concluded that faunas associated with *Myriophyllum* and *Callitriche* in a mountain spring stream differed in terms of relative abundance.

Bryophytes have also been shown to exhibit distinct invertebrate communities. They can be dominated by meiofaunal Nematoda, Chironomidae, oligochaeta, Ostracoda, Copepoda, Acari and Tardigrada (Suren 1991, 1993) and by different macro-invertebrates depending upon the degree of submergence in water (Cowie and

Winterbourn 1979). A number of species have been linked specifically to bryophytes in New Zealand. The tipulid *Limonia hudsoni* and Trichopterans *Zelandopsyche ingens* and *Oeconesus similis* are known to utilise mosses for food (Suren and Winterbourn 1991) and the caddisflies *Zelolessica cheira* and *Pycnocentria gunni* are regarded as primarily moss dwelling (Winterbourn et al. 2000). The main trophic role of bryophytes however, is that they trap fine detritus and provide substrata for diatoms and other algae that are eaten by invertebrates.

Dense macrophyte and bryophyte growths may also influence stream habitats indirectly either by the alteration of dissolved oxygen concentrations in streams (see. 1.2.6. Dissolved oxygen) or through their effects upon hydraulic microhabitat. O'Hare and Murphy (1999) compared invertebrate populations within and around dense stands of *Callitriche stagnalis,* in a Scottish river. They found distinct differences in the diversity and abundance of taxa between weed and riffle habitats, and also between the outer, mid and root sections of the macrophyte stands. They attributed these differences to a combination of habitat structure and water velocity effects.

In a recent review of invertebrate substratum relationships, Death (2000) concluded that despite a relative paucity of evidence New Zealand stream invertebrate communities exhibit different assemblage structures across broad substrate categories, e.g., rocky vs. weedy, but weaker patterns within substrate types, e.g., different weed species. The likelihood that spring communities are influenced by the presence of macrophytes and bryophytes is extremely high, either through their role as substrata, a

food resource, or via their indirect influence on diel oxygen fluctuations and hydraulic micro-habitat diversity.

1.2.8 Longitudinal changes

The physical characteristics of springs described above are indicative of the eucrenal or spring source zone. The boundary between the eucrenal and hypocrenal is dictated by environmental conditions along the spring brook and the relative degree of groundwater to surface-water dominance downstream. With increasing distance from a source, the influence of ground-water diminishes and the stream becomes physically and biologically more like a run-off based stream. The scale of changes, and extent of the eucrenal zone, are determined by precipitation, the morphology of the spring channel and catchment (McCabe 1998). Furthermore, the physicochemical zonation within springs fluctuates over time.

Discharge generally increases downstream, although in some cases there may be a loss of flow back to the aquifer or to the atmosphere, particularly in arid regions (McCabe 1998). Fluctuations in discharge increase with the degree of surface-water influence, thus, levels of physical disturbance may increase with distance from the source. Fluctuations in temperature, used to define the eu- and hypo-crenal zones, also increase with distance from the source. Diel fluctuations as high as 20ºC were recorded 19 m from the source of a California spring brook (Resh 1983), however, in the high discharge spring brook at Waikoropupu the maximum increase in temperature at 110 m from the source was 0.8°C on a hot sunny day (Michaelis 1974). The magnitude of diel temperature fluctuations is influenced therefore, by distance from the source and the absolute discharge of the spring. Increased groundwater

discharge extends the stabilizing influence of the spring, and may offset the effects of surface-water input, heating from solar irradiance or freezing during winter (Smith and Lavis 1975). Longitudinal water chemistry changes are varied but water that initially mimics groundwater conditions will become more like water of overland origin, due to uptake of nutrients by macrophytes and algae, and contact with allochthonous organic matter (McCabe 1998). Dissolved oxygen concentrations maybe low at the spring-source, but rapidly reach saturation upon exposure to the atmosphere (Lindegaard 1998).

The longitudinal zonation of spring brooks bought about by these changes in physical conditions exhibits diurnal, seasonal, stochastic, and weather related, fluctuations, which form a physical template for the biological communities within spring-sources and along spring brooks. Longitudinal variation in benthic communities have been observed in numerous studies (Noel 1954, Sloan 1956, Minshall 1968, Resh 1983, McCabe and Sykora 2000).

1.3 The biological communities of springs

1.3.1 Regional filters of spring benthos

The composition of local biological communities across a landscape are the result of multiple interacting filters operating at different spatial and temporal scales (Poff 1997). The literature on springs reveals at least two sets of primary filters that might affect invertebrate communities; glaciation and local physico-chemical conditions. Glaciation is a large spatial and temporal disturbance, which filters the species pool through destruction of habitat and shifting of environmental and ecological zones (Neiman and Lively 2004). The historical legacy of glaciation has been implicated in the presence and absence of crenobiontic and crenophilous taxa in spring systems

(Nielsen 1950, Sykora and Weaver 1978), and the relative proportions of taxa with different powers of dispersal (Glazier 1991, Williams et al. 1997, Hoffsten and Malmqvist 2000).

Glacial relict taxa are purported to have colonised an area rapidly after the cessation of glaciation. However, due to requirements for specific thermal conditions they were supplanted in surface-fed streams which continued to warm, and they persisted only within the unique and limited habitat of springs. The occurrence of glacial relict species has been proposed in both Europe (Nielsen 1950), North America (Sykora and Weaver 1978), and New Zealand (Michaelis 1974). Nielsen (1950) noted the presence of two Trichoptera species from the great springs of Himmerland, in Northern Jutland. *Apatidea muliebris* and *Parachiona picicornis* are both restricted entirely to springs, and whilst the larvae of the former species are known to be intolerant of temperature higher than those found in the springs, it was not possible to confirm that it was the effects of temperature, or of competitive exclusion by species found in the eurythermic, streams that restricted *Parachiona picicornis's* range. In New Zealand Michaelis (1974) encountered a population of the caddisfly *Rakiura vernale* within the Waikoropupu springs, at the northern tip of the South Island. At that time the species was known only from Stewart Island off the southern coast of the South Island, and Michaelis suggested that *Rakiura vernale* was a glacial relict requiring the cooler temperatures of more southern latitudes or spring waters (Waikoropupu exhibits a constant temperature of 11.7°C). Subsequently, this helicopsychid caddisfly has been found in numerous forested streams on the West Coast of the South Island and it is unlikely that its presence in Waikoropupu Springs is indicative of it being a glacial relict (pers.comm. Harding 2004).

The most recent glaciation in the Northern Hemisphere has been suggested as the reason for a north/south gradient in the presence of amphipods, and other non-insect tax in springs (Williams and Williams 1998), and their absence from springs at high latitude and altitude. Thus, springs in Denmark (Lindegaard 1998) and England (Smith et al. 2003), de-glaciated several thousand years earlier than those in Sweden (Hoffsten and Malmqvist 2000), are dominated by amphipods whereas insect taxa are found further north. Similarly recently de-glaciated, high altitude springs in Spain, are populated by insects which have greater powers of dispersal than the non-insects found in lowland springs (Barquin and Death 2004).

1.3.2 Local filters of spring benthos

Local filters of taxa present within a particular spring include many of the physical factors discussed earlier, and a number of other determinants such as substrate type (Ilmonen and Paasivirta 2005) and flow permanence (Smith and Wood 2002). However, the relative importance of any variable is constrained by its biogeographic setting and interactions with other variables. The unusual conditions and limited spatial area of springs have created unique and enigmatic biotic communities that are a valuable part of regional biodiversity (Di Sabatino et al. 2003).

1.3.3 Patterns of spring benthos

The benthic invertebrate communities of springs exhibit some recurring, although rarely universal, patterns. At the spring source communities may be dominated by

crenobionts and crenophilous species. Crenobionts comprise imigrants from aquifer dwelling populations, such as the New Zealand amphipod *Paraleptamphopus subterraneus* (Chapman and Lewis 1976), or surface-water species restricted by physico-chemical factors to spring habitats, for example the Danish Trichopteran *Apatidea muliebris* MacLachlan (Nielsen 1950). Further along the spring brook lotic, lentic and ubiquitous species become more prominent (McCabe 1998).

Secondly, due to the effects of either sub-optimal physico-chemical conditions, or competitive exclusion, greater diversity of invertebrates in North American and Spanish springs has been shown to occur, downstream (Sloan 1956, Minshall 1968, Ward and Dufford 1979, Barquin and Death 2004). In contrast a number of New Zealand studies have found the opposite pattern of higher diversity at stable sites (Death 1995, Death and Winterbourn 1995, Barquin and Death 2004). However, whereas stable springs had higher diversity than less stable hill slope streams, spring-sources had lower diversity than their brook. The increase in diversity and abundance away from the spring-source was suggested by Barquin (2004) to be the result of changes in substrate composition, stability and invertebrate drift.

Thirdly a survey of 28 North American springs revealed that whilst non-insects dominated hard-water limestone springs, relatively acidic soft water springs were dominated by insect taxa (Glazier 1991). In contrast, studies in Sweden and the England (Hoffsten and Malmqvist 2000, Smith and Wood 2002) recorded dominance of insect taxa irrespective of water hardness. Barquin and Death (2004) noted that whilst the majority of their Spanish springs were dominated by non-insect taxa, primarily amphipods and snails, certain springs showed a shift to insect dominance.

In the absence of differences in site water chemistry, they concluded that the shift was due to either greater flow variability at insect dominated sites, or was a legacy of glaciation, since the insect dominated sites had been more recently glaciated than non-insect dominated sites.

In New Zealand an intensive study of springs by Michaelis (1974) revealed further contradictory results. A number of the patterns discussed above can be addressed using Michaelis's data, although unfortunately only presence/absence data exist for springs other than Waikoropupu (Table 1). The present discussion is therefore limited primarily to issues of taxonomic dominance rather than abundance. Glazier (1991) suggested that hard water springs would be dominated by non-insect taxa. Waikoropupu and Hayes Spring near Queenstown, constitute hard water springs, however whilst the later is insect-dominated, Waikoropupu exhibits an equal number of insect and non-insect taxa. In support of Glaziers (1991) argument, however, 88-96% of all invertebrate individuals found in Waikoropupu Springs were the mollusc *Potamopyrgus antipodarum*. Conversely, soft water springs are expected to be dominated by insect taxa and this was true for Hamurana (Rotorua) and Three springs (Fairlie) but, not for Western Springs (Auckland). Barquin and Death (2004) suggested the legacy of historic glaciation may influence the abundance and presence of some taxa. The six springs considered by Michaelis (1974) are spread equally between the North and South Islands of New Zealand. During the most recent period of glaciation (the late Otiran glaciation 20,000 – 18,000 years ago) much of the South Island but, not the North Island was covered in snow, ice and sparse alpine vegetation, such that many of the modern forest podocarps were restricted to the North Island north of Auckland (Stevens 1981). A gradient of insect to non-insect

dominance in springs might be expected to be correlated with the magnitude of glaciation, south to north, due to the relatively greater time taken for non-insect taxa to colonise. Michaelis's (1974) southern most site, Hayes Spring is insect dominated as predicted, as is the next most northerly site, Three Springs. The central site, Waikoropupu springs is taxonomically balanced between insect and non-insect taxa, and two of the three North Island sites show a shift to non-insect dominance. Thus, it seems reasonable to conclude that in contemporary New Zealand both the biogeographic influence of historic glaciation, and localised physicochemical characteristics influence spring invertebrate communities.

Discharge velocity has also been suggested to have an affect upon community composition in springs (Barquin and Death 2004). Unfortunately, velocity data are only available for different zones within Waikoropupu Springs. Overall the spring system contained an equal number of insect and non-insect taxa, which were numerically dominated by the mollusc, *Potamopyrgus antipodarum* (88-96%). However, at sites with higher water velocity and fewer macrophytes all non-insect taxa were reduced in abundance, *Potamopyrgus antipodarum* falling to 56% of the total individuals (Michaelis 1974).

Table 1. Numbers of insect and non-insect taxa compared to physico-chemical conditions found at 6 spring sites in New Zealand by Michaelis (1974). Sites are listed from south to north. - = no data.

	South Island			North Island		
	Hayes Spring	Three springs	Waikoropupu	Otangeroa	Hamurana	Western Springs
Insect	6	8	21	3	11	2
Non-insect	4	3	21	4	3	4
pH	neutral	neutral	neutral	neutral	neutral	neutral
Conductivity (µs cm^{-1} 25°C)	196	low	650	-	79	251
Hardness	hard	soft	mod. hard	-	soft	soft
Geology / Water origin	karst	riverine karst	karst	-	volcanic/high silicates	volcanic/high silicates

Death et al. (2004) reported only 12 non-insect taxa out of 104 taxa collected in a regional spring survey. However, the majority of these sites were at greater than 300 m a.s.l. The role of altitude in this community shift may be related to any one of the reasons stated above, the geological context, water physico-chemistry, the legacy of historic glaciation, local habitat conditions or possibly a gradient of anthropogenic impact from lowland to alpine environments.

In summary, patterns of taxa specificity, diversity and community composition observed within and between springs and spring brooks are the result of hierarchical filtering operating at different spatio-temporal scales (Poff 1997). The available species pool at any point will be imposed upon the physicochemical template of the spring type and can be expected to account for the differences observed between studies in the Antipodes, North America and Europe.

1.4 Springs in the flood plain landscape

1.4.1 Riverine landscapes

Understanding the mechanisms regulating patterns of species occurrence and abundance is a principal aim of ecology. Classical ecology focused on ecological processes affecting populations and communities operating at local scales. Recently there has been an increasing awareness of the importance of processes acting at larger scales, such as the landscape. A landscape is the mosaic of habitat patches within which the focal patch is embedded, and is generally considered at a spatial scale intermediate between an organism's normal home range and its regional distribution (Dunning et al. 1992). Landscape ecology considers the impact of spatial pattern on ecological processes (Wiens 2002).

Recently, there has been a move towards applying the principles of landscape ecology to riverine systems, specifically to fluxes across terrestrial/aquatic ecotones and to heterogeneity that exists within the river itself (Wiens 2002). The concept of patch dynamics is an integral part of landscape ecology that has been successfully applied to freshwater environments (Pringle et al. 1988, Townsend 1989). Consideration of mosaics of variable habitat quality across a landscape are particularly applicable to the study of flood plains, which often exhibit high spatial and temporal habitat diversity (Ward et al. 2002). Braided river springs might be considered as patches of high productivity embedded within a matrix of terrestrial and low productivity main channel habitat (Digby 1999), or as aquatic islands of stability within a sea of disturbance. The flux of energy, materials and individuals between patches and/or the matrix have important ramifications for the ecology of the riverine system.

Alluvial flood plains make good model systems for investigating landscape processes. They contain a diversity of landscape elements which exhibit high degrees of connectivity across three dimensions, and dynamism over time. Surface-water, terrestrial zones including riparian vegetation and the stygoscape (alluvial aquifer) are all part of an interacting mosaic of habitats, which impact upon the biotic communities living within (Jones and Mulholland 2000). To fully understand the ecology of a dynamic riverine system it is important to consider the complete hierarchy of effects from the climatic and geological setting, through reach geomorphology, to local patch productivity and biotic processes (Poole 2002).

The twin themes of ground-water, surface-water exchange and hydrological connectivity have received particular attention in recent years, and the centrality of

their role in regulating nutrient dynamics (Dahm et al. 1998), oxygen availability (Malard and Hervant 1999), riparian vegetation (Huggenberger et al. 1998, Pusch et al. 1998) and biotic communities (Brunke and Gonser 1997, Malard et al. 2002) has been investigated. Hydrological exchange occurs within the setting of a dynamic successional landscape mosaic. Surface-water habitats, including spring brooks, in a flood plain reach of the Tagliamento River in northeast Italy exhibited 62% turnover after a single flood season (Arscott et al. 2002). Aquatic habitat composition, however, remained stable supporting the applicability of a shifting mosaic steady-state model to flood plain corridors. Thus despite high turnover of habitats, the proportions of one habitat type to another remained the same (Arscott et al. 2002).

A complete reworking of the flood plains of alpine rivers has been estimated to require between 150 and 250 years for rivers in British Colombia and New Zealand (Reinfelds and Nanson 1993). If we assume that the long term re-working of a flood plain surface complies with the steady state model described above, we would expect to find aquatic habitats varying widely in age at any point in time. Successional patterns in spring invertebrate communities should be regulated by the age of the site, the variable dispersal powers of invertebrates and the dispersal paths available to them. The time since major disturbance of a site is particularly interesting in the case of the crenobionts with no aerial dispersal capabilities. The New Zealand amphipod *Paraleptamphopus subterraneus* and the flatworm *Prorhynchus putealis* can only disperse through groundwater flow paths, however the degree of genetic isolation of sub-populations, or ability of these organisms to utilise the aquifer for dispersal is unknown. In Germany the gastropod *Bythinella dunkeri* and flatworm *Crenobia alpina* are restricted to springs but, potentially use groundwater to disperse between

surface habitats. Measurement of gene flow between populations of the two species using allozymes provided a proxy measure of dispersal. *B. dunkeri* appeared to have higher gene flow when compared to *C. alpina*, which had more isolated populations, suggesting that *B. dunkeri* may use groundwater flow paths as a dispersal route (Brandle et al. 2005). Further it could be inferred that the presence of a crenobiont in a relatively young braided river spring habitat indicates its use of ground-water flow paths for dispersal.

Flood plain reaches of alpine rivers exhibit high levels of aquatic habitat area, ecotone length, thermal and substrate heterogeneity (Arscott et al. 2000), compared to more constrained reaches. This is reflected in the high levels of taxonomic diversity found across flood plains (Robinson et al. 2002). A study of benthic assemblages over time and across habitat types in the braided Val Roseg River, Switzerland, showed that whereas unstable main channel habitats exhibited high temporal variability in invertebrate densities, spring-fed streams contained different communities that were more stable over time (Burgherr et al. 2002). Hydrological connectivity across flood plains creates aquatic habitats that contrast strongly with the main river channels and to hill slope streams that feed the main channels. As a result higher diversity at the landscape scale is bought about through the utilisation of spring habitats by invertebrates unable to inhabit the main channel and hill slope streams. In addition it is likely that springs and spring brooks provide refuges for benthic invertebrates during high flows (Burgherr et al. 2002), and play an important role in source-sink dynamics between sub-populations across riverine landscapes (Caudill 2003, Donahue et al. 2003).

1.5 Concluding remarks

Springs are an interesting phenomenon, embedded within a variety of landscapes from high mountains to lowland flood plains. Their up-welling groundwater creates aquatic habitats, which often exhibit physicochemical conditions that contrast greatly to surface fed streams and ponds. Generally, springs have a stable discharge regime, constant temperatures, elevated but stable levels of ionic enrichment and sometimes low levels of dissolved oxygen. The sudden exposure of spring water at the surface results in rapid gradients in these variables along the outflow channels, the steepness of which is related to surface conditions. Within the physical template of these springs and spring brooks are found biotic communities, some of whose members are found only in such habitats. Consequently springs constitute an important part of river corridor biodiversity. The unique conditions found within springs have been used for the testing of ecological theory, however, there is considerable confusion over the true drivers of community structure within spring-source sites. Springs and spring brooks within the flood plains of large rivers are an important part of the aquatic habitat available across the landscape. Hydrological connectivity across flood plains increases habitat and biotic diversity. The precise role of springs and the nature of their interaction with other braided river habitats are vital to obtaining a holistic understanding of braided river ecology.

1.6 Thesis Outline

The primary aims of this research were three-fold. Firstly, I wished to consider the large scale occurrence and distribution of springs within the catchments of 20 braided

rivers. Secondly, I wanted to assess the contribution of spring habitats to overall taxonomic diversity in the braided river corridor. My final aim was to investigate the drivers of spring benthic invertebrate community structure.

Chapter 1, of this thesis consists of a review of the current knowledge of cold water springs, with a particular emphasis on springs that occur within the alluvial flood plains of braided rivers. Chapter 2, involved a mapping survey of 20 braided river catchments. The relationship between springs, catchment, reach and local scale geomorphic features were explored. Chapter 3, deals with the contribution of springs to river corridor diversity, and involves a faunistic comparison of hill slope streams, main channels and springs. In chapter 4, a range of physicochemical conditions are considered in relationship to spring invertebrate communities. Potential drivers of invertebrate community structure are identified. Chapter 5, involved a manipulation of macrophytes within spring-sources. Macrophytes appeared to be important in structuring invertebrate communities, therefore shifts in community metrics resulting from the removal of macrophytes were observed. Chapter 6, considers the ramifications of my findings in the context of ecological stability and anthropognic impacts upon braided river systems.

2

Braided river springs: occurrence, distribution and mechanisms – A GIS approach

2.1 Introduction

2.1.1 Braided rivers: characteristics and elements

Braided rivers occur globally, in arctic and alpine regions with a distinct flood season, in arid and Mediterranean climates subject to torrential rain, and in some tropical regions subject to monsoonal rains (Bravard and Gilvear 1996). The braided rivers of the South Island of New Zealand have been formed over the last 20,000 years as a result of glacial action, rainfall and snow melt (Gage 1977). These riverine environments are the result of continuous erosive processes, friable bedrock, and high and unpredictable levels of precipitation. The rivers are characterised by large, unpredictable floods, and due to the low timber line (1200-1500m), steep terrain and extensive scree slope formation, by some of the highest sediment yields reported for any rivers in the world (Winterbourn et al. 1981). Consequently the wetted bed of the river constantly changes location, and the river fauna are adapted to life in a highly disturbed, physically unstable, aquatic system.

A defining characteristic of a braided river is an extensive, flat, alluvial flood plain which, may range in width from hundreds of metres to in excess of 20 km in the case of the Brahmaputra River, Bangladesh (Bristow and Best 1993). Across these flood plains the active channel of the river migrates back and forth. Flood plains are recognised as being extremely patchy environments in terms of successional stage and habitat structure (Poole et al. 2002). The active river channel is highly unstable, but is bounded by a mosaic of more stable elements, which have been classified according to their sedimentary deposits (Bravard and Gilvear 1996), or vegetational succession (Burrows 1997).

Recent alluvial deposits typically have high hydraulic conductivity allowing the formation of an alluvial aquifer and high levels of groundwater surface-water exchange (Woessner 2000). The movement of water through the alluvium is determined by hydraulic pressure, depositional structure and the parent lithology of alluvial deposits (Stanford and Ward 1993, Valett et al. 1996, Woessner 2000). Their conductivity results in a blurring of the perceived boundaries of the river and consequently, flood plains comprise a wide variety of aquatic habitats, many of which are linked via surface and sub-surface flow paths. The concept of hydrological connectivity includes the complete range of linked aquatic habitats, and an image of a single body of water moving at variable speeds via multiple pathways through the flood plain system.

One obvious consequence of high connectivity is the occurrence of flood plain springs. These springs exhibit physico-chemical characteristics in complete contrast to the river main channel and constitute an important habitat within the riverine landscape (Burgherr et al. 2002, Ward et al. 2002).

2.1.2 Catchment scale determinants of local phenomena

"*In every respect the valley rules the stream*" (Hynes 1975)

Catchment scale influences on streams are a conceptual theme that can be traced back to the original statement of Hynes (1975). However, it is only in more recent times that technological advances have enabled the linkages between landscape-scale factors and lotic systems to be measured and tested (Johnson and Gage 1997, Harding et al. 1998, Wiens 2002, Townsend et al. 2003). The physical form of a stream or flood plain is influenced by a variety of landscape features operating at a range of

scales (Figure 1). Many of these features exhibit feedbacks and are inter-correlated. The concept of this spatio-temporal nested hierarchy of interactive elements is well described in the literature (Frissell 1986, Poff 1997, Poole 2002), but there are few examples of specific links between landscapes and local habitats (Richards et al. 1996, Harding et al. 1998).

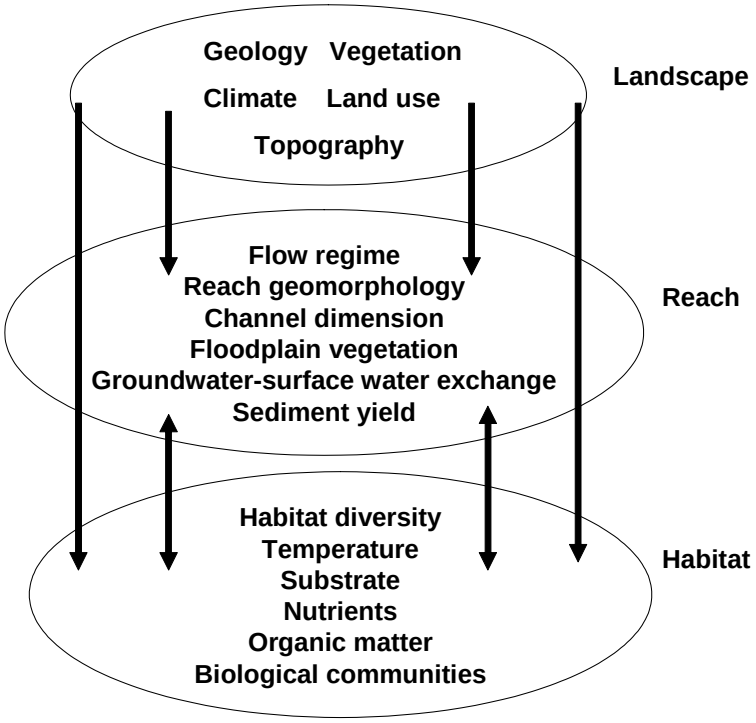

Figure 1. A conceptual model of the hierarchical linkages between catchments and local habitats. Feedbacks might include nutrient retention influences upon riparian vegetation, but primarily the local habitat is determined by conditions operating at larger reach or catchment scales.

Geomorphologists have a long history of recognising the trans-scale links within catchments (Chorley et al. 1984). Extensive removal of vegetation in the catchments of Australian river systems has resulted in downstream changes in depositional patterns and drastic changes to flood plain morphology (Prosser et al. 2001). The large scale effects of vegetational cover are also neatly illustrated by a comparison of

two headwater flood plains of the Tagliamento River, in N.E Italy (Arscott et al. 2003). The flood plains were similar in terms of altitude, stream order, geological context and position in the longitudinal continuum of the river, however, whilst one flood plain was stable and forested, the other was un-forested and consequently more dynamic. Investigation of local habitat structure, and physicochemical conditions revealed significant differences between flood plains within their differing large scale contexts, with the forested reach exhibiting a lower slope, finer sediment and more standing water (Arscott et al. 2003). In the Saginaw Basin of Lake Huron in East-Central Michigan a raft of landscape variables describing climate, geology, topography, land use and hydrology were related to the reach scale physical habitats found to exert the greatest influence upon stream communities. The two catchment scale variables, proportion of lacustrine clays and glacial outwash materials were found to have considerable influence upon reach characteristics (Richards et al. 1996). The effects of catchment driven sediment supply and discharge on reach scale morphology have been described (Lane and Richards 1997). However, the modification of these effects by existing reach scale morphology indicates that complex feedbacks occur within dynamic systems (Chorley et al. 1984).

The geological context of a catchment dictates the nature of flood plain alluvium. In a comparison of hydrological conductivity between North American flood plains of differing material, a sandstone-silt catchment exhibited low conductivity (1.3×10^{-4}cm/s), whereas a granite-gneis catchment showed much higher conductivity (4.1×10^{-3} cm/s) (Morrice et al. 1997). The amount of surface-water/groundwater exchange increased with hydrological conductivity, therefore it is intuitive to expect the number

and density of springs within a flood plain would be linked to the bedrock derived alluvium of which it is composed.

2.1.3 Reach and local scale

The conceptual perspective illustrated in Figure 1 shows the linkages between reach, or intermediate scale processes, with the diversity of local habitat types (including springs). A number of studies have invoked valley or bedrock constrictions, tight bends, and impermeable sediment layers with the up-welling of groundwater within alluvial river corridors (Stanford and Ward 1993, de Jong and Ergenzinger 1995, Malard et al. 2002). Other studies have highlighted the relationship between aquifer stage height, historic braid channels and the sheltering effect of sediment deposition (Poole et al. 2002). Reach geomorphology is also known to respond to changes in slope, whereby, given constant sediment loadings and flow regimes, river channel morphology is predictable on the basis of slope (Bravard and Gilvear 1996).

2.1.4 The New Zealand context

Very little is known about the distribution and occurrence of braided river springs in New Zealand. However, Reinfelds and Nanson (1993) made an extensive investigation of stable flood plain elements within the Waimakariri catchment and they found that the most extensive stable areas occurred in the lee of outcropping bedrock or alluvial tributary fans. These sites were characterised by mature successional vegetation and numerous spring brooks which flowed within the depressions formed by abandoned braid channels. Such streams, existing on stable, sheltered areas of flood plain may remain undisturbed by river migrations for long

periods of time. Reinfelds and Nanson (1993) suggested a period of 250 years may elapse before the entire Waimakariri flood plain is re-worked. However, not all springs will be situated on flood plains sheltered to this degree. For example Digby (1999) described the formation of baseflow spring streams and baseflow seepage streams, the later carrying surface-water during periods of high discharge, in the lower reaches of the Rakaia River. The seepage streams were short lived, whereas the spring streams were more permanent and located outside the main channel network. The spring streams, however exhibited intermittent flow at periods of low discharge in the main river suggesting that they too were not necessarily stable throughout the year.

New Zealand is an ideal place to study braided river springs because many rivers with braided reaches, are located throughout the South Island. High quality Geographical Information System (GIS) data also exist, which describe terrain, land cover, geology and climate. In addition, detailed topographical maps (1:50 000 km) have been produced of the entire country, based on aerial photography (Land Information New Zealand 1995).

2.1.5 Objectives

The objectives of this study were to document the occurrence and distribution of braided river spring-sources in 20 catchments in the South Island of New Zealand. The catchments chosen all exhibited braided reaches along their lengths, but varied in geology, vegetational cover, climate and topography. Catchment areas ranged from the small, but steep Waitaha River, 332 km^2, to the much larger Wairau River, 3700 km^2. The Tasman River catchment is 30% covered in ice and 68% tussock, whereas,

the Arawata River and Landsborough River are 50% forest and approximately 20% tussock. The geology of the catchments varied, but consisted primarily of greywacke, schist and gneiss. Mean annual rainfall ranged from 8.2 m in the Arawata River to 1.5 m in the Wairau River. The numbers of springs found in each catchment also varied markedly, from 2 in the Awatere River to 69 in the Rakaia River.

I had three primary objectives for this chapter:

1. To map the distribution and occurrence of springs in braided river catchments across the South Island of New Zealand.

2. To model catchment scale characteristics that might be used to predict the occurrence of springs.

3. To identify reach scale characteristics that might be important for determining occurrence of springs.

2.2 Methods

2.2.1 Spring Identification

I mapped 20 braided river catchments in the South Island (Figure 2), then located and digitized spring-sources into ARC GIS (8.0). Springs were identified by eye from "topo" maps (1:50000 km), (Land Information New Zealand 1995) as channels arising on the river flats with no surface link to a recognizable hill slope stream or upstream connection to the main river. Spring permanence was indicated by the presence of vegetation, particularly around the spring source, and used to distinguish spring channels from backwaters and flood channels with an intermittent upstream connection to the main river. Spring-sources were also classified according to the valley type within which they occurred (confined or flowing across plains), and

according to any natural or man-made features with which they appeared to be associated, e.g. tributary fans, bluffs or flood retention works. A considerable number of springs occurred on vegetated islands within the main channel network of rivers, and were classified as being exposed to the destructive, flood plain element eroding effects, of the river. The classification was qualitative but, consistent across catchments.

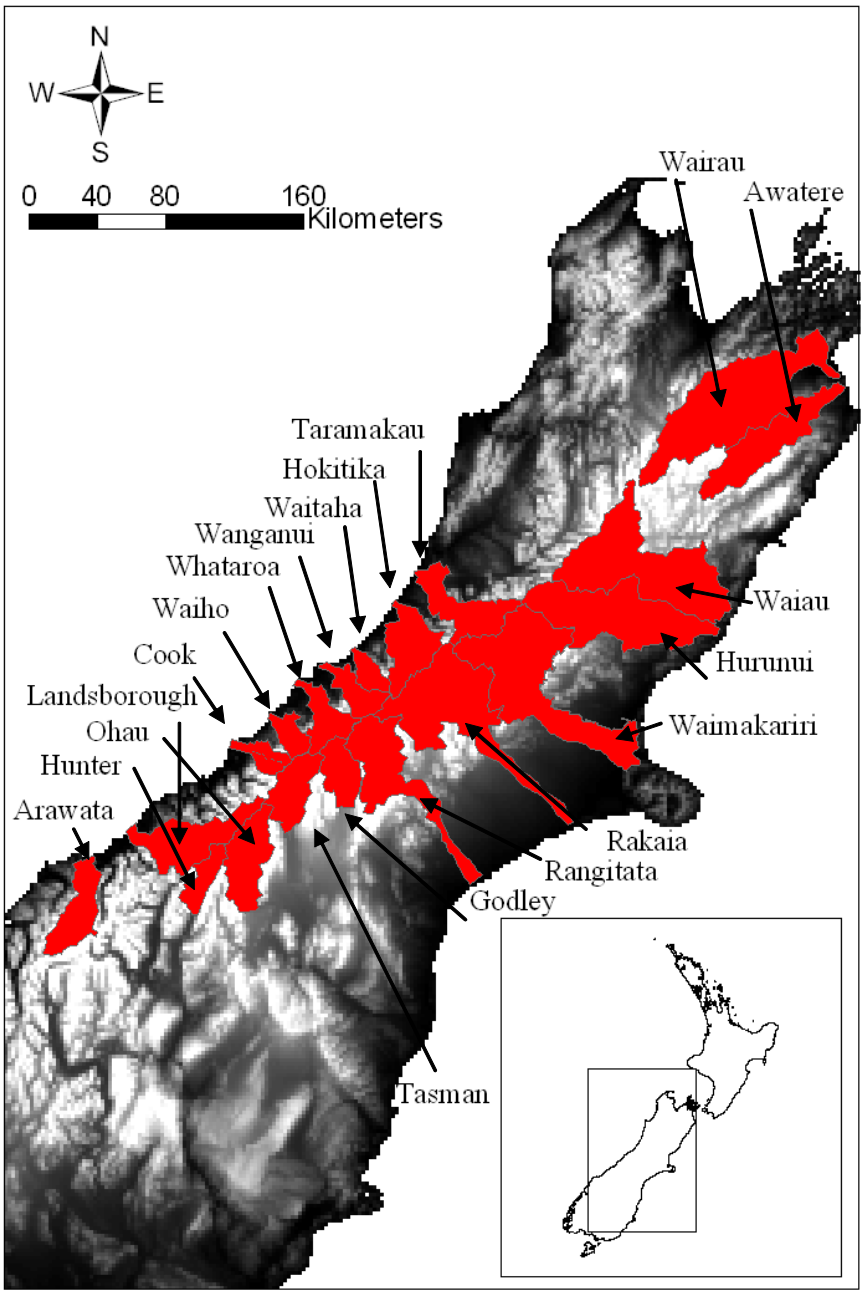

Figure 2. South Island of New Zealand showing the 20 braided river systems analysed in this study. Catchments were delineated using the hydrological modelling tool within ARC GIS 8.2 (Environmental Systems Research Institute, Redlands, CA, USA.) and the New Zealand 500m Digital Elevation Model.

2.2.2 Catchment scale

Catchments of each of the 20 rivers were modelled using a 500 m resolution Digital Elevation Model (DEM) and a cell based hydrological modelling tool within ARC GIS 8.0 (Environmental Systems Research Institute, Redlands, CA, USA.). The catchment areas were then used to extract landscape variables from various digitised data resources. The New Zealand Land Resource Inventory (LRI) provided geological data for catchments which were converted to a percentage of catchment area. The New Zealand Land Cover Data Base 1, version 2 provided data on ice, bare ground and vegetation type (Figure 3 A).

A river corridor can be viewed as consisting of three nested elements, the flood plain, active river bed, and the wet bed (Figure 3 B). The ratios between these elements can be used as descriptors of the river environment (Robinson et al. 2002, van der Nat et al. 2003). If the active river bed is considered to be the area regularly reworked by flooding, its relationship to the area of flood plain represents a measure of disturbance in the corridor. Flood plains were modelled using elements from the New Zealand Land Cover Data Base by combining the area of flats alluvial deposits, and the river channel itself. The active river bed constituted a Land Resource Inventory element entitled “river channel”, and represented regularly re-worked gravels. Comparisons were made to “topo” map (Land Information New Zealand 1995) and aerial photos to evaluate the efficacy and accuracy of this assessment. Finally, the area of the wetted bed of the river came from the Land Cover Data Base. The Land Cover Database was created from aerial photos taken during periods of fine, stable weather, when rivers are close to base flow. The ratio of active river bed to base flow wetted bed also provided a measure of geomorphological conditions in the river corridor. Thus,

higher the ratio the greater the magnitude of dynamism, a river with small base flow that re-works a large expanse of gravel must experience extreme flood events.

Grid data for elevation (South Island 25m DEM), slope (calculated from the SI 25m DEM) and rainfall, digitised from Metservice maps (1985) for the entire South Island were overlain with catchment areas, to allow the derivation of means and coefficients of variation (CV) for each catchment. Finally, the mean and CV for slope of each flood plain were extracted by overlaying the slope grid and the flood plain area.

Table 2. Catchment scale variables derived using GIS. Some variables such as the nested flood plain elements underwent further synthesis prior to analysis.

Variable	Measurement	Source
Geology	% Cover	New Zealand Land Resource Inventory
Vegetation	% Cover	New Zealand Land Cover Data base
Wetted bed area	Km^2	New Zealand Land Cover Data base
Active river bed area	Km^2	New Zealand Land Resource Inventory
Flood plain area	Km^2	New Zealand Land Cover Data base
Annual rainfall	Metres	Metservice maps (1985)
Catchment Elevation	Metres	New Zealand 25m DEM
Catchment slope	Degrees	New Zealand 25m DEM
Flood plain Slope	Degrees	New Zealand 25m DEM

Statistical analysis

A Pearson correlation matrix, analysed in Systat (2000), identified variables that showed a significant relationship ($p < 0.05$) with spring density across the catchment after normalisation. Regression analysis was then used to test the significance of the relationship. Principal Components Analysis (PCA) in Systat (2000), was used to decompose variables into groups representing combinations of significant variables.

2.2.3 Reach scale

Profiles of each river system (n=20) were generated by digitising points along the river. The altitude of each point was measured using the SI 25m DEM and the

horizontal distances between points were measured using a distance tool (ARC GIS 8.0). The number of springs upstream of a point and below the previous one was recorded and slopes calculated.

In order to compare reach slope between confined valleys and the plains, flood plain polygons for the four East Coast, South Island rivers containing both confined valleys and open plains (Hurunui, Waimakariri, Rakaia, Rangitata) were dissected. The areas and mean slope were then re-calculated.

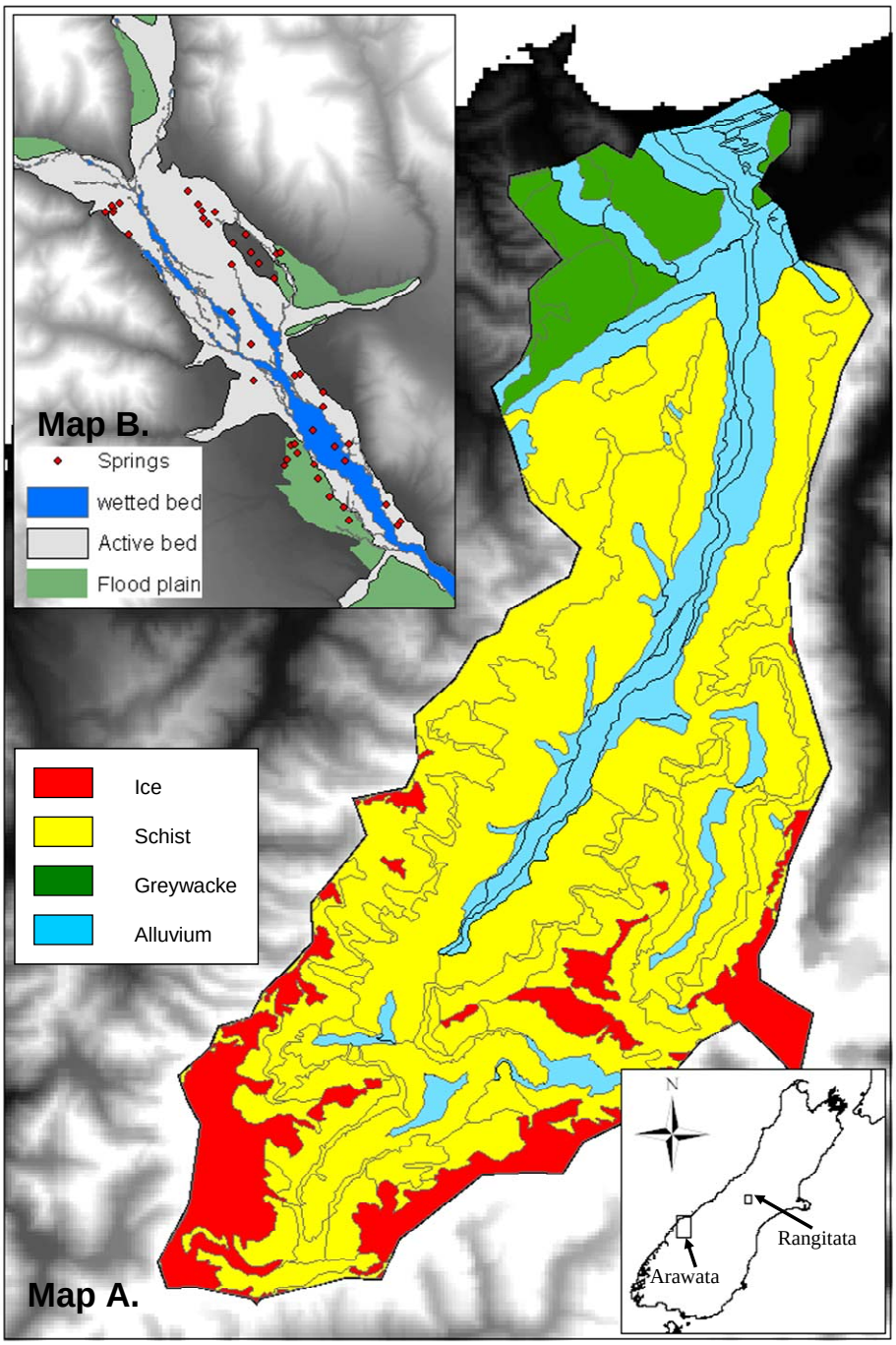

Figure 3. Derivation of catchment variables. Map A shows the geology and distribution of ice cover which defines the Arawata catchment in South Westland, New Zealand. Geology data was extracted from the Land Resourse Inventory database using ARC GIS 8.2 (Environmental Systems Research Institute, Redlands, CA, USA.). Map B illustrates the nested elements that occur within flood plains, and spring sources within the Rangitata catchment. See text for explanation.

2.2.4 Local scale

Slope data were generated from individual catchment 25m DEMs and sampled using the position of each spring. Each cell in the grid was 25 x 25 m, and the slope of the grid was calculated as the greatest difference between that cell and those adjacent to it. The slope at each spring site represented the figure for the single cell that contained that point.

2.3 Results

2.3.1 Catchment scale

A Pearson correlation matrix (Systat 2000) was used to identify catchment variables which showed a significant relationship, with spring density. The only variable to do so was mean annual rainfall (-0.493), (Figure 4). The strength of this relationship was tested with regression analysis.

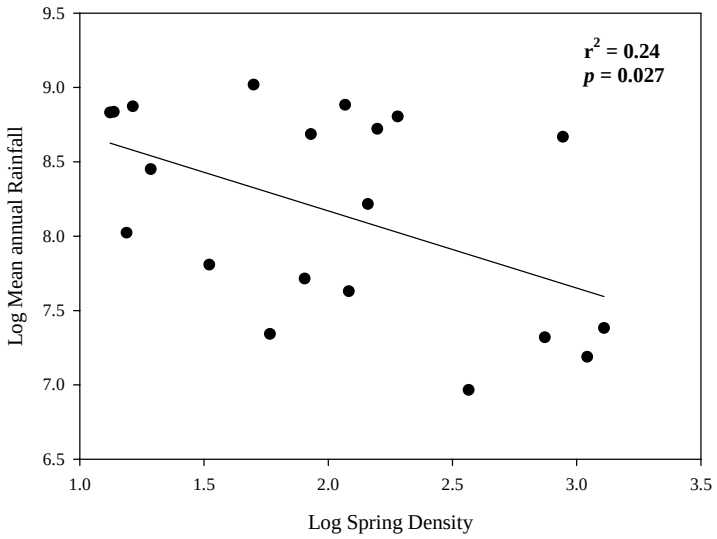

Figure 4. Regression of Log spring density on Log mean annual rainfall.

To allow for the fact that large scale variables may be acting in concert on river corridor geomorphology the entire data set was decomposed using PCA. A further

correlation matrix of factor scores versus spring density, revealed no further significant relationships.

Table 3. r^2 and *p* values for a regression of catchment variables against log spring density

Variables	r^2	*p*
Mean rain	0.24	0.03
Flood plain/active river	0.02	0.57
Flood plain/wetted bed	0.06	0.29
Active river/wetted bed	0.01	0.70
% Greywacke	0.10	0.17
% Ice	0.04	0.38
% Forest	0.12	0.13
% Tussock	0.07	0.28
% Bare ground	0.00	0.78
Mean altitude	0.01	0.64
Altitude CV	0.04	0.37
Mean slope	0.14	0.11
Slope CV	0.01	0.73

2.3.2 Reach scale

River profiles were generated for all catchments and the number of springs within each reach recorded on a secondary y axis. Springs occurred at points along the river with slopes of less than 0.9 degrees (Figure 5). The large, east coast, South Island rivers Rakaia and Waimakariri, contained braided sections in their upper reaches, in which springs occurred. However, the Arawata and Whataroa rivers flowed through gorges in their upper reaches which precluded the formation of springs. Thus, springs only occurred where flood plains were deposited.

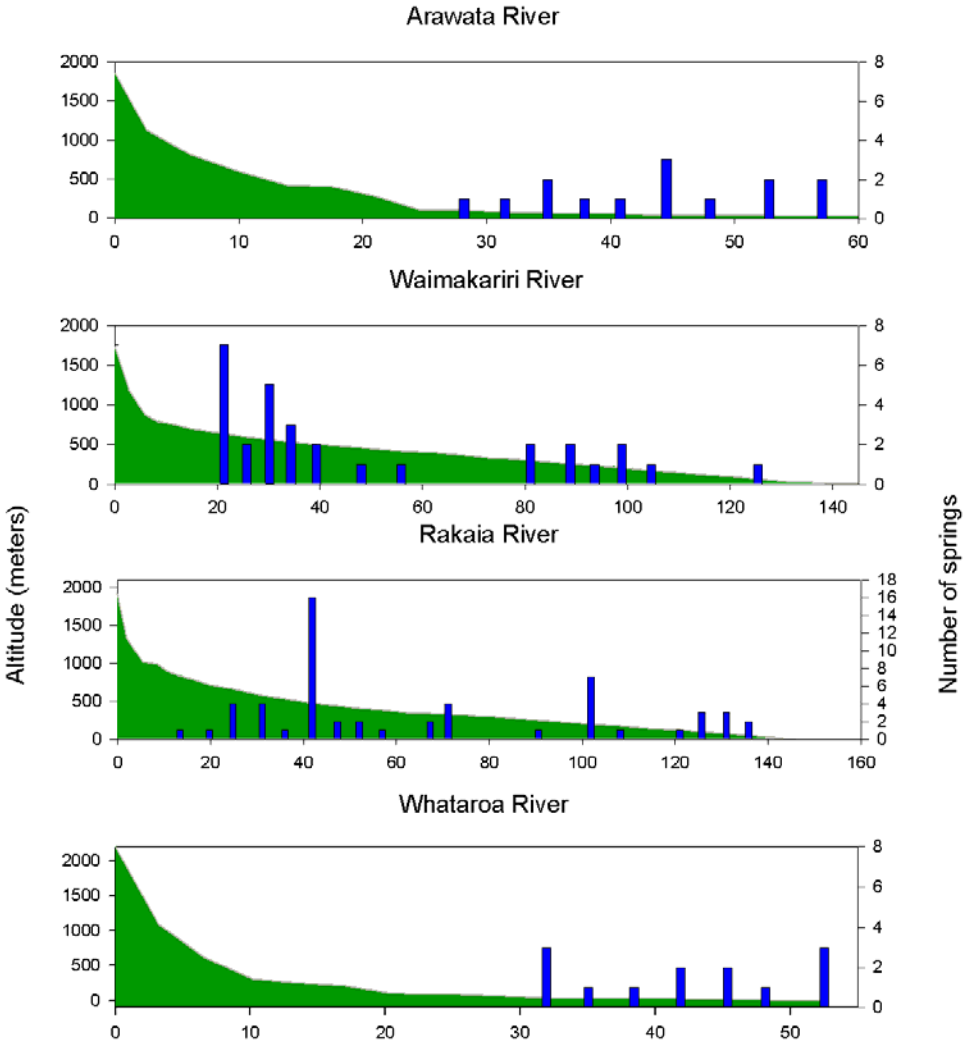

Figure 5. Longitudinal profiles of four major rivers showing the position of springs within the catchment (kilometres from source) and the density of springs within braided river flood plains.

The river profiles show the location of springs along the rivers and enabled reach slope calculations to be made and related to the occurrence of springs. Mean reach slope for springs in all catchments was between 0.1 - 0.9^{o} (Figure 6). However, when the Tasman River springs, which occur at the base of a glacial moraine on steep ground, are excluded, the range of slopes is only 0.1 - 0.5^{o}.

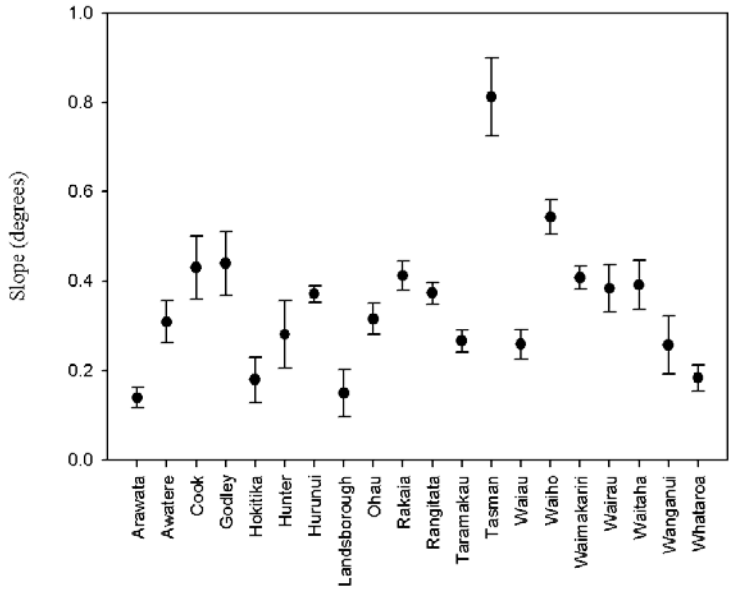

Figure 6. Mean (±1 S.E.) reach scale slope at spring sites.

Three eastern South Island rivers, which contained both confined and unconfined reaches, were used to test for differences in the slope of spring-containing reaches in the two valley types (Figure 7). No significant difference was found between the slope of spring containing reaches in confined and plains reaches, except in the Rakaia River where the unconfined reaches had a lower gradient. Across all three rivers the slopes observed in each of the two valley types were very similar.

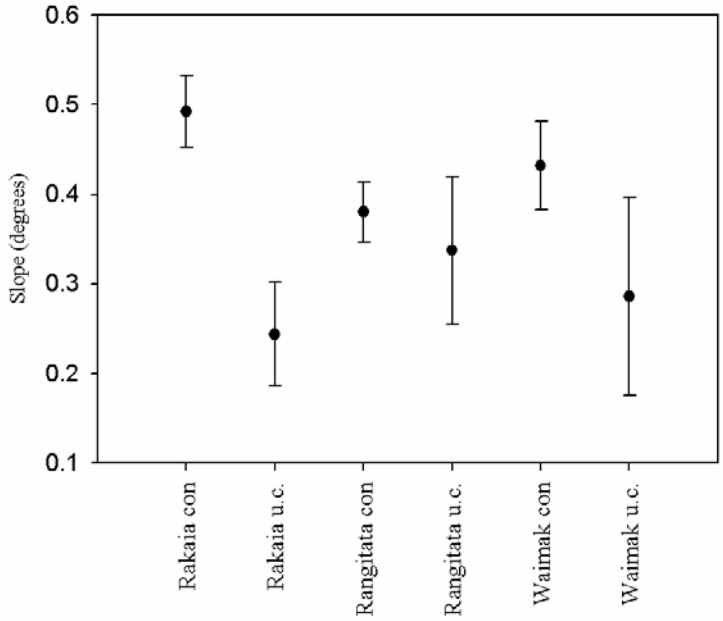

Figure 7. Mean (± 1 S.E.) reach slope in three east coast rivers, confined (con) and unconfined (u.c.) reaches.

The number of springs in different valley types within braided rivers differed consistently with more springs being found in inland, confined valleys than on the plains. (Table 3). The actual density of springs, calculated as the number of springs divided by flood plain area, exhibited the same pattern (Figure 8).

Table 4. Spring number, density and the area of flood plain in confined and unconfined alluvial valleys.

River	Valley type	Spring No.	Flood plain area	Spring density sp/km^2
Waimak	Plains	9	82.96	0.11
	Confined	26	64.59	0.40
Rangitata	Plains	9	38.70	0.23
	Confined	52	142.24	0.37
Rakaia	Plains	17	135.84	0.13
	Confined	52	192.14	0.27

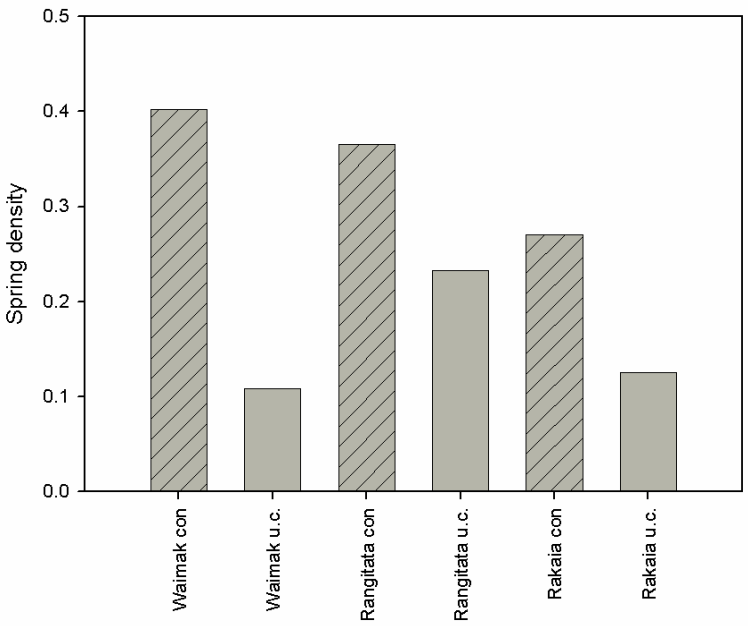

Figure 8. The density of springs (number of springs / flood plain area) in confined (con) and unconfined (u.c.) reaches of three east coast rivers.

2.3.3 Local scale

Reach scale (2-3 km) slope measurements may not reveal distributional patterns if spring density and occurrence are determined by local scale phenomenon. Therefore, local slope (slope of the 25 m grid square within which the spring source located) was calculated for each spring site (Figure 9). Mean local slope for spring-sources in each river ranged from 0 to 1.2^{o}.

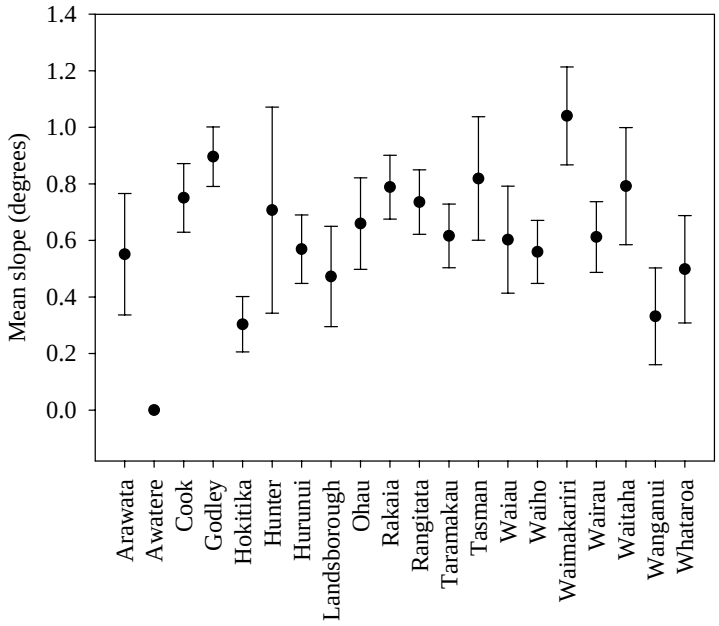

Figure 9. Mean (± 1 S.E.) local scale slope of individual springs in 20 South Island rivers.

Mean reach slope and mean local slope at spring sites exhibited similar amounts of variation across catchments. Therefore, the differences in spring density in the confined and unconfined plains reaches of braided rivers could not be attributed to differences in slope at the reach or local scale. The possibility exists that spring density is affected by local geomorphological features such as bluffs and alluvial fans.

2.3.4 Geomorphology

Springs were classified further according to their proximity to geomorphological features which might influence up-welling (Table 4). These specific features were selected after an examination of maps and spring systems in the field.

Table 4. Percentages of springs associated with flood plain elements.

Fan	Bluff	Flood works	Exposed
29	20	16	35

Across all catchments, almost 50% of springs occurred in the shelter of an alluvial fan or bluff (Figure 10), and a further 16% occurred in the lee of man-made flood retention works (Figure 11). In total 65% of springs were associated with some form of obstruction in the river corridor whereas the remaining 35% were in mid channel sites and therefore, were exposed to flood events within the river.

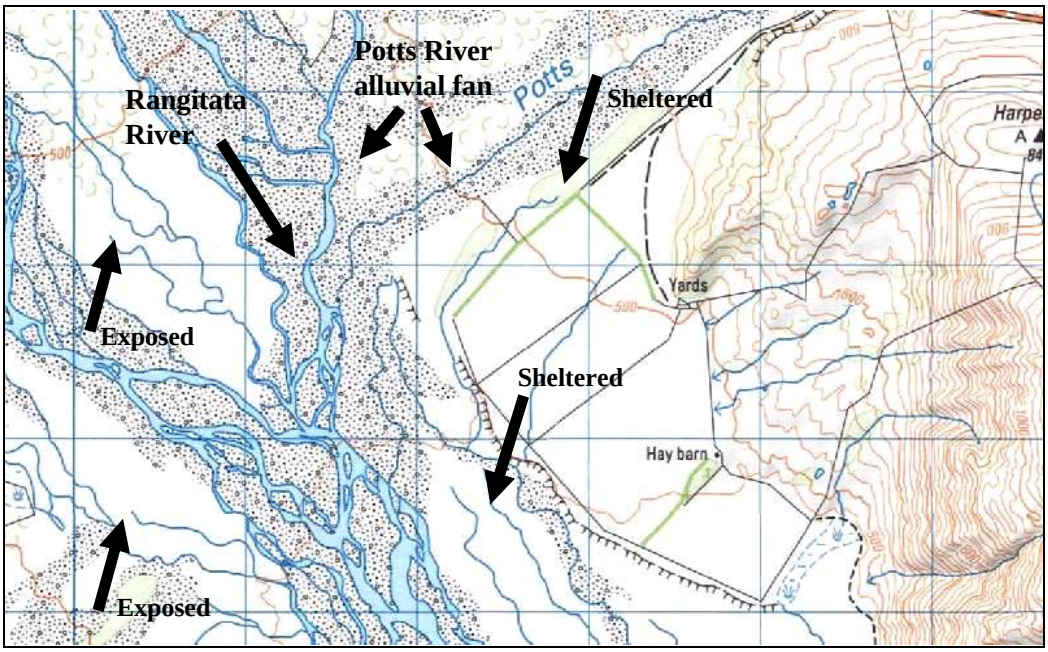

Figure 10. Alluvial deposits from the Potts River shelter the springs in the centre of this map from the larger Rangitata River. Exposed springs arising on a vegetated island can be seen to the left of the map.

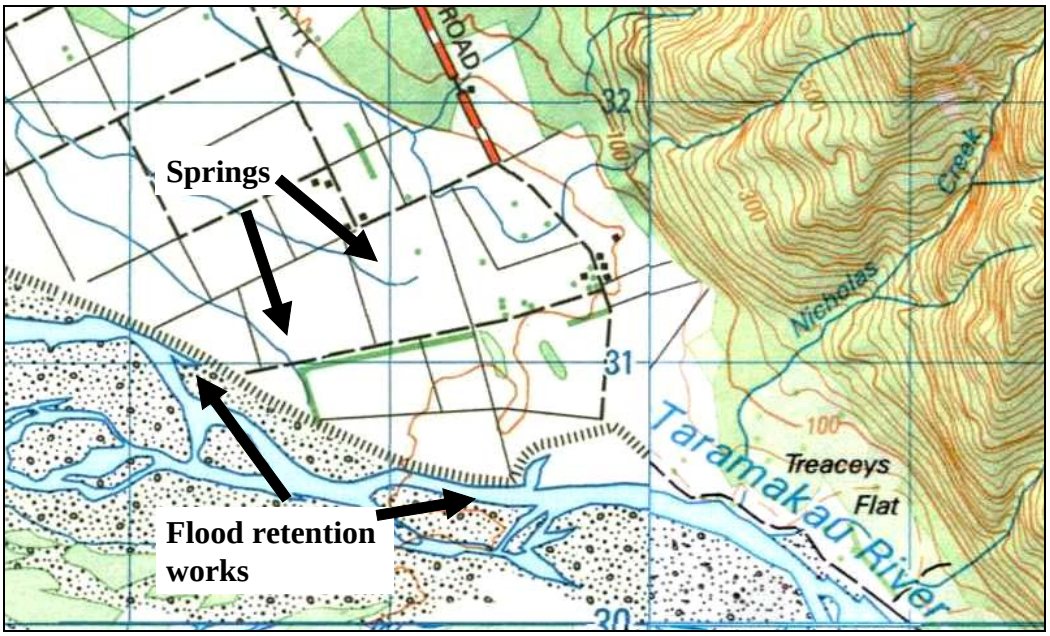

Figure 11. Flood retention works on the Taramakau River protect large areas of agricultural flood plain from the erosive forces of the river. Springs arise in the paddocks and re-join the main river several kilometres downstream.

Spring sites not associated with geomorphic obstructions in the valley, i.e. exposed sites, were found throughout the braided corridors of four east coast rivers (Table 5). In confined valleys they comprised between 18-26 % of springs. However, in reaches on the plains approximately 90% of springs occurred in exposed sites, with only springs associated with flood retention works in the Waimakariri River preventing this figure being higher.

Table 5. Percentages of springs found in association with flood plain elements in confined and plains reaches of four east coast, South Island rivers.

	Fan	Bluff	Flood works	Exposed	n
Hurunui confined	70	10	0	20	10
Hurunui plains	0	0	0	100	9
Rakaia confined	47.1	29.4	2	21.6	51
Rakaia plains	0	0	0	100	17
Rangitata confined	44.2	37.2	0	18.6	43
Rangitata plains	0	0	0	100	9
Waimakariri confined	55.6	11.1	7.4	25.9	27
Waimakariri plains	0	11.1	0	88.9	9

In confined reaches, exposed springs represented a smaller percentage of the total spring numbers than in the plains reaches. However, actual numbers (Table 6) suggest that in at least three of the four catchments, exposed springs were as likely to be found in confined reaches as plains reaches. Whilst fans and bluffs are "by definition" absent from plains reaches, they contribute to high overall numbers of springs in more confined reaches.

Table 6. Numbers of springs associated with different geomorphic features in confined and plains reaches of four east coast rivers.

	Fan	Bluff	Flood works	Exposed	Total
Hurunui confined	7	1	0	2	10
Hurunui plains	0	0	0	9	9
Rakaia confined	24	15	1	11	51
Rakaia plains	0	0	0	17	17
Rangitata confined	19	16	0	8	43
Rangitata plains	0	0	0	9	9
Waimak confined	15	3	2	7	27
Waimak plains	0	1	0	8	9

The percentage of springs associated with each feature is shown for each catchment in Figure 12. No single feature was associated with all springs in any one catchment. Flood retention works contributed the largest percentage (approx. 40%) of springs in

the large West Coast rivers, Hokitika, Taramakau and Wanganui. Most springs were found on outwash plains close to the sea where flood retention works had been constructed to protect farmland. Exposed (approx 30%) and bluff (approx 20%) springs occurred in similar numbers in most catchments, but fan sites were more common in east coast rivers.

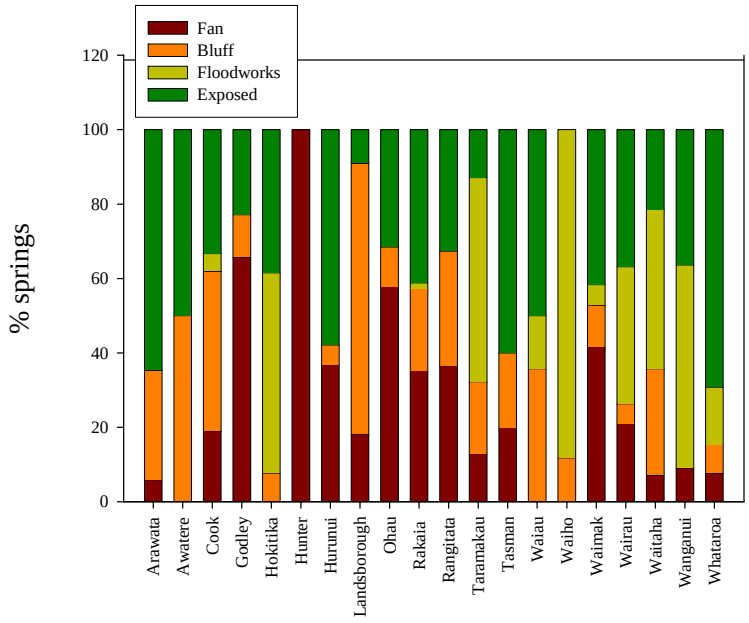

Figure 12. Percentage of springs in each catchment associated with different flood plain elements.

2.4 Discussion

2.4.1 Catchment scale

Little correlation was found between landscape variables and the occurrence of springs. The lack of correlation can be attributed to one of three things. Firstly, that springs are not an ideal measure of local river geomorphology. It is intuitive to think that the local form of a river may be regulated by the catchment within which it is contained, such that variation at the catchment scale would correlate to variation at the reach and local scale. However, the presence or absence of a spring may not measure

the subtle changes in local flood plain geomorphology that are predictably driven by catchment geology or vegetational cover.

Secondly, the variables derived from the GIS, and the techniques used to analyse them may have been insufficient to describe the variation which does drive river morphology across a catchment. A GIS-derived variable is only as good as the data on which it is based, usually broad scale aerial photos, or geological surveys. If source data lack adequate resolution, then so will any derived variables used for analysis. Geology, vegetation, climate and topology, have all been considered in this analysis but, it is highly likely that these variables act on river morphology in concert. For instance, Arscott et al. (2003) found that in two rivers with comparable topography and climate, river morphology differed due to vegetational cover of the catchment. However, the affect of vegetational cover presumably would also differ between catchments having different climates. If so, the effects of both these variables on local river morphology would be altered by variations in geology and topology. Consequently, the mechanistic links between the catchment and the local scale are extremely complex, diffuse, and difficult to analyse.

Thirdly, springs may be a local rather than a catchment scale phenomenon. River corridors have been regarded as longitudinal continua with aquatic habitat changing predictably, depending upon position along the continuum (Vannote et al. 1980). However, discontinuities, for example between an alluvial flood plain and a gorge, disrupt and reset the longitudinal continuum (Poole 2002). Catchment characteristics may dictate the range of river environments that are possible, but reach, and nested within them, local scale characteristics, define those which exist. If such an

hierarchical system of landscape filters exists (Frissell 1986, Poff 1997), and springs are a locally regulated phenomenon, then a describable link between the catchment scale and spring density would be difficult to detect.

A significant relationship was found in my study between mean annual rainfall and spring density. An obvious dichotomy among catchments involving rainfall would be to split the low rainfall east coast South Island sites from the high rainfall west coast ones. Although point three (above) argues against landscape scale causal mechanisms, it is interesting to note that the considerably wetter, west coast rivers exhibit a lower density of springs. However, reference to Figure 12 reveals the predominance of springs sheltered in the lee of flood retention works on west coast alluvial plains. The stability of these springs in the absence of flood retention works is a moot point and therefore, the density of naturally occurring west coast flood plain springs is bought into question.

2.4.2 Reach scale

Rivers have been classified into functional sectors, or reaches using a variety of hydrological and geomorphological criteria. An important criterion driving the formation of braided reaches is slope. Braiding is found in valleys with a gradient of 0.04 to 0.17^{o}, with an abundance of bed material and a hydrological regime marked by major flood peaks (Bravard and Gilvear 1996).

The South Island rivers profiles (Figure 5) show the occurrence of springs is closely related to slope and when profile data were decomposed to provide mean reach slope at spring sites (Figure 6) catchment means and standard errors fell within the slope

boundaries of Bravard and Gilvear for the formation of a braided bed. Interestingly, no springs were recorded in braided reaches exceeding 0.9^{o}. Possibly the reaches exhibiting braiding above 0.9^{o} and below the posited braiding maximum slope of 1.7^{o} are too unstable for the development of vegetated flood plain elements, and associated stable spring creeks. These steeper sites tended to be closer to the headwaters in mountainous country and were on rivers tightly constricted by steep valley sides, and experiencing high bed load inputs from unstable hill slopes.

A further breakdown of the data set to compare mean reach slope of confined and unconfined river reaches (Figure 7) revealed little difference between the valley types within and between rivers. However, Table 5 shows consistently higher densities of springs in the confined sections of river valleys. Presumably, this is not the result of a difference in slope characteristics between reaches and rivers.

2.4.3 Local scale slope

The patterns of local slope at the site of up-wellings are consistent with those at the reach scale. Up-welling sites appear to be on low gradient sites representative of the reaches within which they are contained.

2.4.4 Spring formation

Stable springs were identified as being the source of streams arising on the river flats amongst vegetation. Therefore, they had been stable, long enough, at the time of mapping, for plants to become established in the river bed gravels. In all, 65% of

these springs occurred below a physical sheltering structure, whereas the remaining 35% appeared to be exposed to disturbance from the river. It is possible that the exposed sites were protected from re-working by resistant vegetation, such as willow trees, or that these stable flood plains are formed by river bed abandonment (Reinfelds and Nanson 1993) whereby, the braid train migrated to another part of the valley floor allowing stabilising vegetation to establish. Such sites are likely to have greater impermanence than sites protected in the lee of an obstruction, as the braid train may well migrate back across the valley floor to its previous location.

Alluvial fans and rocky bluffs are unusual along plains reaches of rivers and few were found on four east coast rivers. Instead, exposed sites increased from approximately 20% of springs in confined reaches to being the predominant type in plains reaches (Table 4). However, in both valley types the actual numbers of exposed springs was very similar (Table 6). The confined reaches of braided rivers contained a greater number and diversity of springs by virtue of the presence of both exposed and sheltered sites.

A comparison of spring types across catchments (Figure 12), and mean reach slope at spring sites (Figure 6), revealed a pattern between slope and spring type. Rivers with a mean slope of less than 0.3 degrees had a higher percentage of exposed sites than steeper rivers. Unfortunately, the pattern was blurred by the effects of flood retention works, particularly in the Taramakau and Wanganui rivers. This pattern suggests that stable, exposed flood plain springs may be more common in lower gradient rivers and is supported by the fact that of the four east coast rivers, the highest number of exposed springs was in the lower gradient Rakaia plains reach (Table 3).

2.4.5 River corridor model

I hypothesis that a longitudinal model of an idealised river corridor containing both confined and unconfined plains reaches will have springs distributed as follows.

a) High gradient upper reaches (0.5-100^{o}, with braiding below 1.7^{o}). Springs will predominantly be found associated with glacial moraine structures as at the Tasman River site.

b) Low gradient confined reaches (0-0.5^{o}). Large numbers of springs will be present due to both sheltering and exposed mechanisms.

c) Low gradient plains reaches (0-0.5^{o}). Fewer springs will be found as only exposed and flood retention works springs are present. The lower the flood plain gradient, the greater the number of exposed springs that are likely to occur.

2.5 Conclusion

Springs within stable flood plain elements are a common feature of braided rivers in the South Island. The links between catchment scale variables and spring density revealed no significant causative patterns despite the intuitive notion that "the stream is ruled by its valley". Although alluvial river beds are known to braid at slopes of between 0.04-1.7^{o}, springs were only found at slopes lower than 0.9 degrees, probably due to the tightly confined and unstable nature of upper reaches. Stable flood plain elements would seem to be associated with four physical factors: shelter behind bluffs, alluvial fans, flood retention works, and more transient sites that occur within

the main river network and are exposed to flooding. Exposed sites occurred consistently throughout the confined and plains reaches of rivers, however, sites sheltered behind bluffs and fans were found almost exclusively in confined valley reaches. Exposed sites were more likely to occur in river reaches with a lower gradient.

Flood retention works, despite blurring patterns in the data were associated with 16% of springs identified. The implications of this are twofold. Whilst it is interesting that human activities can be constructive as well as destructive in terms of habitat and therefore, bio-diversity, it also raises concerns about the extent of our knowledge of the long-term effects of activities such as gravel extraction and flood bank construction.

Inter-montane confined valleys contain the greatest density of springs and diversity of spring types and therefore, represent the ideal places in which to study the contribution of braided river springs to biodiversity.

3

The contribution of springs to river corridor bio-diversity

Photo: Duncan Gray

3.1 Introduction

The physico-chemical conditions within a stream form a template, which defines the biological communities that inhabit them (Quinn and Hickey 1990a, Winterbourn 2004). The presence or absence, and relative abundance of taxa are a direct result of individual, community and population responses to habitat conditions in the stream environment. The aquatic habitats within the flood plain reaches of braided rivers are characteristically diverse and incorporate extremes of disturbance, productivity and stability (Death 1991, Digby 1999, Ward et al. 1999a, Arscott et al. 2002, Robinson et al. 2002). The main channel or channels of New Zealand braided rivers are characterised by unstable substrate, high sediment yields, regular shifting of the wetted bed and large, and unpredictable floods (Griffiths 1979a, Winterbourn et al. 1981). Braided rivers characteristically flow across extensive alluvial flood plains. This alluvium is highly permeable and allows river and surface-water to percolate down into the flood plain aquifer (Woessner 2000). The aquifers frequently also have zones of up-welling, which create spring habitats within the braided river flood plain. Connectivity between the main channel and springs is mediated by the aquifer and creates highly contrasting habitats. Springs exhibit stable flows, high productivity and relatively constant physicochemical conditions (McCabe 1998, Digby 1999). Mountainous reaches of South Island braided rivers are also fed by numerous hill slope streams which have their own unique set of physico-chemical conditions.

Although New Zealand stream communities have been regarded as containing a core of generalists (Winterbourn et al. 1981), many taxa do exhibit marked habitat preferences. The broad range of freshwater habitats found across New Zealand are

occupied by taxa that are well adapted to unstable or extreme environments (Thompson and Townsend 2000). New Zealand's most common mayfly the leptophlebiid, *Deleatidium* reaches its highest density in disturbed, stony streams (Sagar 1983, 1986, Scrimgeour 1987, Quinn and Hickey 1990a). In contrast, the caddisflies *Zelandopsyche ingens* and *Oeconesus* spp. prefer small forested streams and seepages, whilst *Zelolessica cheira* inhabit mosses and bryophytes in swift, rocky streams (Winterbourn et al. 2000). The phreatic flatworm *Prorhynchus putealis* and amphipods of the genus *Paraleptamphopus* are generally restricted to underground waters and springs (Percival 1945, Chapman and Lewis 1976). Thus we recognise that contrasting habitats can contain different invertebrate communities.

A mapping survey of 20 New Zealand river catchments (Chapter 2) revealed that spring complexes are a typical feature of braided flood plains. The highest density of springs was found in inter-montane basins, which contain extensive alluvial flood plains bounded by steep valley sides. Although spring complexes were found on the flood plain, exposed to the river, they were more commonly found in the shelter of tributary alluvial fans, rocky bluffs, and man-made flood retention works. Both these natural and constructed features disrupt the movement of the river across its bed. The upper Waimakariri River, between its confluence with the Crow and Poulter rivers was seen to exhibit all these features (Figure 1). Therefore, this section of river was chosen for a comparison of the physical and biological characteristics of habitats within braided river systems.

Environments that are more spatially heterogenous can be expected to accommodate more taxa because they offer a greater variety of microhabitats, a greater range of microclimates, and refuges from disturbance and predators (Begon et al. 1996).

If we accept that high habitat heterogeneity within the braided rivers corridor contributes to high levels of biodiversity, then we might ask how unique are the communities within these habitats, and which habitats contain the greatest amount of biodiversity?

The objectives of the research presented in this chapter were:

1. To quantify differences in the physical environment of the three braided river corridor sub-habitats: main channel, spring, and hill slope stream.
2. Examine differences between the benthic invertebrate communities within these habitats.
3. Determine the relative contribution of each sub-habitat to the overall biodiversity of the braided river corridor

3.1.1 Study area

The Waimakariri River is one of several large rivers that flow east from the glaciated main divide to discharge into the Pacific Ocean along the Canterbury coastline (Figure 1). The river is approximately 150 km long, with a catchment area of 3560 km^2 (Reinfelds and Nanson 1993). The catchment can be separated into two distinct geomorphic units. The mountainous upper catchment (2490 km^2) contrasts dramatically with the predominantly flat, coalesced glacial outwash fans that form the Canterbury plains (Bal 1996). Many headwater tributaries are glaciated (6.5 km^2) and the catchment has a maximum elevation of 2408 m (Mount Murchison).

Lithologically, the catchment is dominated by approximately 45% Greywacke sandstone, the remainder comprising localised limestone, volcanics, conglomerate, coal measures and substantial areas of alluvial and glacial outwash deposits (NCCB 1986). Mean annual flood flows in the Waimakariri River (gauged 5 km from the sea) is 1520 m^3s^{-1}, with a probable maximum flood of 8000 ± 1000 m^3s^{-1}, and mean annual flow of 121 m^3s^{-1} (NCCB 1991, Reinfelds and Nanson 1993). Average annual rainfall declines along a steep west to east gradient , from about 5000 mm at the main divide to less than 1000 mm at the base of the foothills (Greenland 1977). Major floods result from heavy rainfall on the main divide associated with low pressure systems in the Tasman Sea and the presence of north-westerly winds. An estimated 11% of annual precipitation in the upper catchment is stored as snow and ice during the Australasian winter and released during spring and summer (October to February) when it contributes about 30% of the flow (NCCB 1986, Reinfelds and Nanson 1993). The river attains periods of base flow most commonly during late summer and mid-winter when stable weather reduces precipitation or allows water to be locked up as snow and ice. However, the maritime nature of New Zealand's weather means that heavy rainfalls can occur at any time during the year, and do so, unpredictably. Compared to many Northern Hemisphere alpine regions New Zealand exhibits a low timber line (1200-1500 m) resulting in considerable areas of many catchments being steep and barren. Above the forest, alpine slopes are often de-pauperate in vegetation due to the combined effects of historic fires, grazing by Red Deer (*Cervus elaphus)*, the friable nature of the bedrock and the unstable state of substrates (Burrows 1977, Winterbourn et al. 1981). The combination of high rainfall and exposed substrate in the form of debris slides results in New Zealand rivers having some of the highest sediment yields of any rivers in the world (Griffiths 1979a). These prevailing

contemporary conditions and the legacy of historic glaciation have resulted in the modern, dynamic, riverscape that we see today.

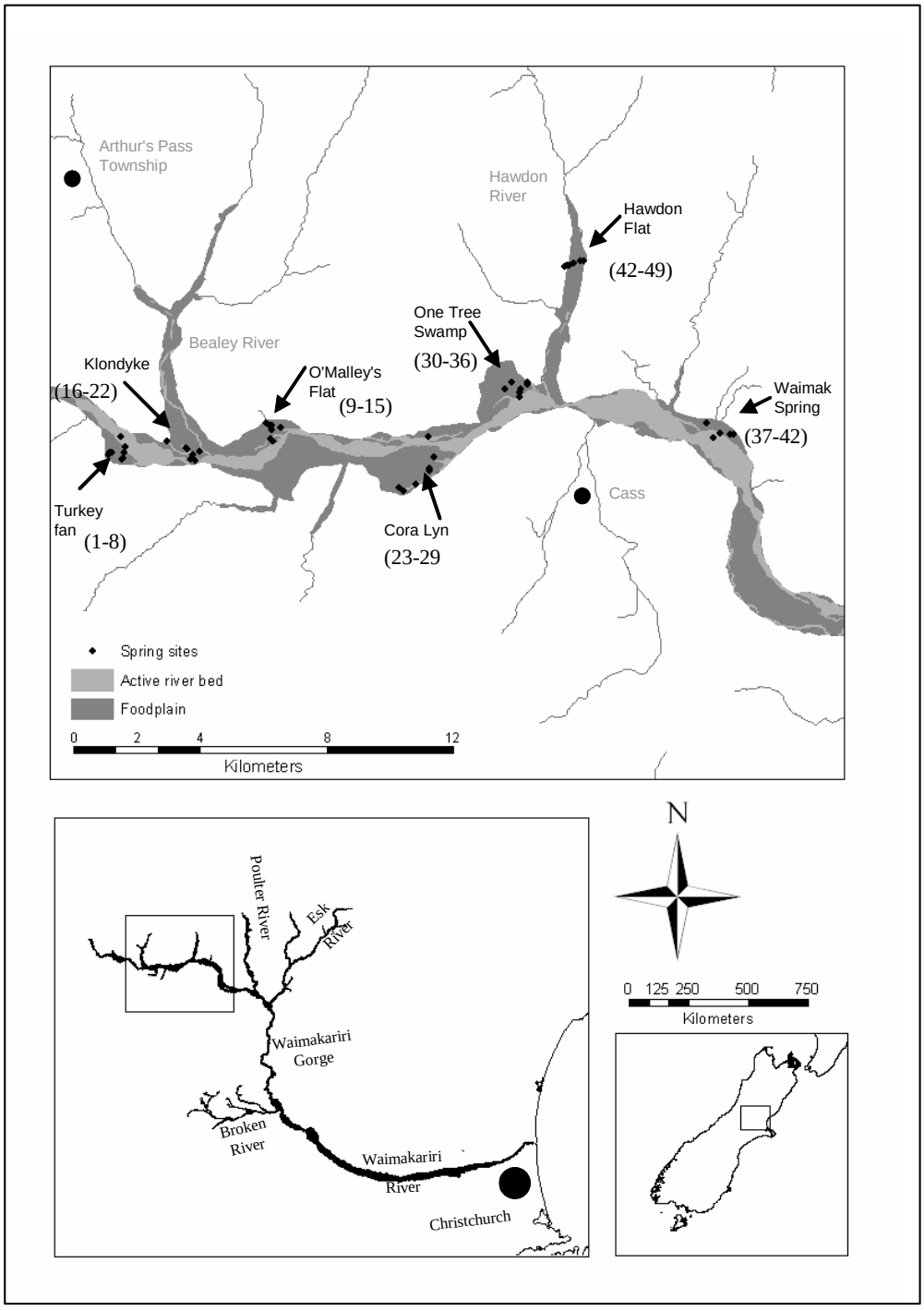

Figure 1. The Waimakariri River catchment showing the location of seven spring complexes with site numbers, hill slope, and main channel sampling sites.

The Waimakariri River flows along a glacially moulded valley (Gage 1977), which forms an extensive alluvial flood plain between the headwaters and Esk River confluence. The river braids across the flood plain, regularly shifting its wetted bed, before flowing into a bedrock gorge (The Waimakariri Gorge) incised up to 300 m (Griffiths 1979b). Below the gorge the river emerges onto the Canterbury Plains and braids once more before reaching the sea to the north of Christchurch.

Above the gorge the Waimakariri River has a number of distinct features, which influence its channel morphology and hydrology. Several large tributaries join the river, forming alluvial outwash fans that protrude onto the braided flood plain (Figure 2). In the shelter of these outwash fans, stable areas of vegetation have developed on the flood plain surface, however, the presence of remnant braid channels on these surfaces indicates that the main river flowed through these areas at some stage. Much of the flood plain, across which the main river currently flows, is devoid of vegetation. The reworked gravels of the active river bed are subject to regular inundation during floods and frequent drying during low flows. A final feature of the Waimakariri flood plain is the presence of spring-fed channels with no upstream connection to the main channel or a hill slope stream. These are obvious in the centre of Figure 2 flowing across the darkened area of flood plain to the right of the Jordan Stream.

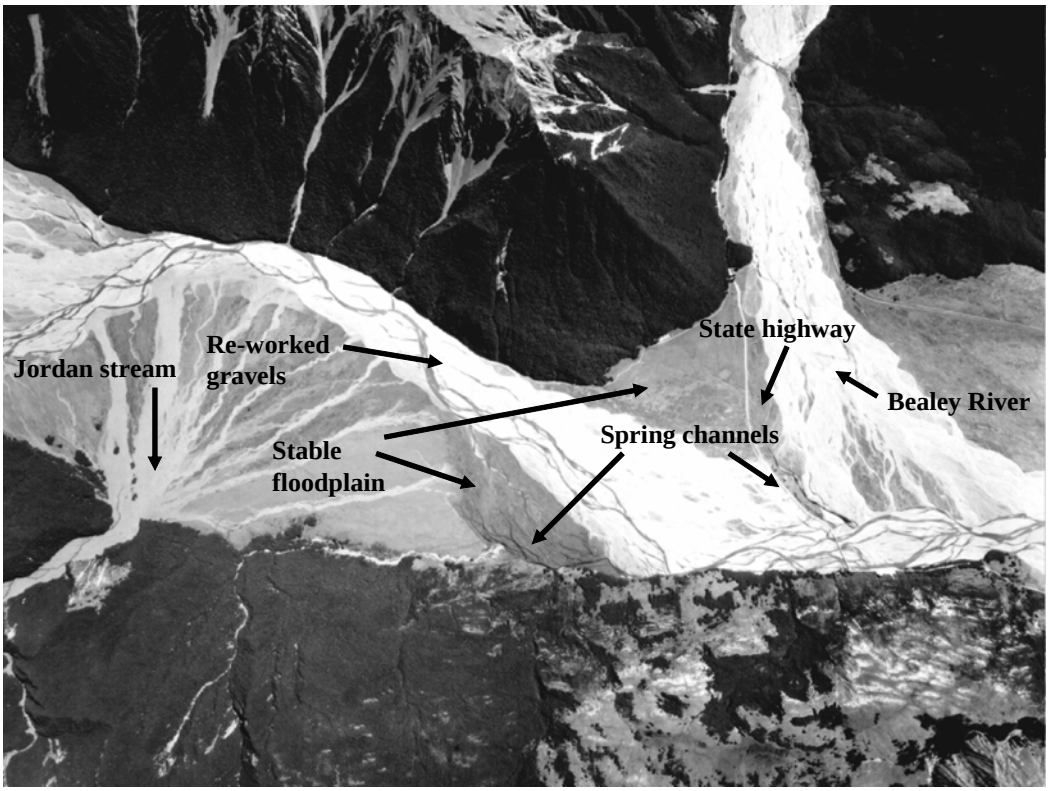

Figure 2. The Waimakariri River at its confluence with the Bealey River. The outwash fan of the Jordan stream is obvious on the left of the photo, whilst several areas of stable, vegetated flood plain border the regularly reworked gravels of the active river bed. The photo was taken during stable weather and baseflow conditions in the main channel, the braided Waimakariri River can be seen in several channels. At the right is the main highway to Arthur's Pass township. Flood works associated with this road have deflected the river to southern side of the valley and created more areas of stable flood plain in their lee. On the flood plain at the centre of the photo can be seen numerous spring-fed channels with no upstream connection to the main channel or hill slope streams. This photo was taken in 1948 and these channels are still in existence today. Permission to reproduce this section of air photograph SN 8584 E/8 was granted by the department of Survey and Land Information.

3.2 Methods

3.2.1 Spring site identification

Up-welling areas were identified using local knowledge, topographical maps (NZMS 260; 1:50,000, sheets k33, k34, l33, l34) and field observations. Seven clusters of springs were found along the study reach, ranging in altitude from 646 to 513 m a.s.l. (Figure 1, Appendix 1 & 2). All springs sampled were independent of each other, no sites were up-stream of another site on the same stream, and sampling was undertaken at points above the confluence of any tributaries. At each cluster an attempt was made to choose springs from across the breadth of types available, taking into account the successional age of the surrounding flood plain, discharge, velocity and substrate. A total of 42 spring sites were sampled and within each cluster a main channel and a hill slope stream site were also sampled.

3.2.2 Benthic invertebrate sampling

Spring and main channel sites were sampled once during June 2004 and again in December 2004. Hill slope streams were sampled once during December 2004. At each site an extensive kick net sample (mesh size 250 µm) was taken over a 10 m reach. All aquatic habitats within the reach were included in the composite sample. Samples were preserved in 70% ethanol in the field and sorted in the laboratory under 40x magnification. Identifications were made from keys by Winterbourn (1973), Chapman and Lewis (1976), Cowley (1978), McLellan (1998), Winterbourn et al.(2000), Smith (2001) and a description by Percival (1945). Identification was carried out to the lowest taxonomic level possible except for oligochaeta which were not differentiated further, and Chironomidae which were not separated below tribe.

Presence/absence and semi-quantitative coded abundance (Stark 1998) were recorded for each taxa at each site.

3.2.3 Environmental variables

Within spring and main channel sites physicochemical sampling of temperature, conductivity, dissolved oxygen, discharge, and flow velocity was performed six times over the seven month period (June to December 2004). Substrate disturbance was measured on the last four sampling occasions, whilst macrophyte cover, substrate composition, stream slope and flood plain element age were recorded once. Hill slope sites were sampled once in December 2004.

Water physico-chemistry

Temperature and conductivity were measured with an Oakton pH/con 10 meter, and a YSI 550A DO meter was used to record dissolved oxygen levels. Readings were taken on each occasion at an established site within the sampling reach.

Discharge

When possible, a single transect located at an area of laminar flow, free from obstructions, was chosen for the estimation of discharge. Discharge was calculated using the velocity-area integration method (Gordon et al. 1992). Flow velocity was estimated by determining the time taken by a cork to move along the stream for a known distance. Measurements were made at 3–5 points across the stream depending upon its width.

Substrate composition

Substrate composition was estimated by measuring the longest axis of 30 particles randomly, at each site and classifying them according to the Wentworth classification (Giller and Malmqvist 1998). From this a substrate index (SI) was calculated. The SI ranges between 3 and 8, (where 3 indicates 100% silt/sand and 8 indicates 100% boulders) (Jowett and Richardson 1990).

$$SI = ((0.03 \times \%silt/sand) + (0.04 \times \%fine\ gravels) + (0.05 \times \%coarse\ gravel) + (0.06 \times \%\ cobbles) + (0.07 \times \%boulders))$$

Bed disturbance

To assess bed disturbance painted particles representing the 50^{th} and 75^{th} quartile of substrate found at each site were placed on the stream bed in riffles. Particles were arranged in two rows, one of five stones representing each particle quartile. The movement of these stones was recorded on four separate occasions between August and December 2005. On each occasion particles that had moved were noted and replaced, as described by Townsend et al. (1997).

Stream slope

Stream slope of a 25 m reach was measured using a Stanley compu-level, which compares the difference in elevation between two points.

Macrophyte, bryophyte and algae cover

Macrophyte, bryophyte and algal percentage covers were estimated by eye for the 10m reach used for invertebrate sampling. No attempt was made to separate bryophyte or algal taxa, however macrophytes were identified to species level using a key by Coffey (1988).

Continuous stage height and temperature monitoring

Stage height, air and water temperature were recorded at four spring sites and in one hill slope stream between 14 July 2004 and 11 December 2004 using TruTrack WT-HR 1000 water height and dual temperature data loggers. Readings were taken every 30 minutes for the entire period. No temperature data are available for the Waimakariri River as the data logger would not survive flooding events. However, stage height data was provided by the Canterbury Regional Council.

3.2.4 Data treatment and statistical analysis

One way ANOVA, and non-parametric Mann-Whitney and Kruskal-Wallis tests were performed in Systat (2000) to test for differences between physico-chemical conditions in streams. Tukeys post-hoc test was used to identify significant differences.

Non-metric multi dimensional scaling (Nmds) was performed to examine patterns in community composition. This was done using the PRIMER statistical package (Clarke and Warwick 1994). Stress values provide a measure of goodness of fit for the ordination with values ranging from 0-1. Values close to 0 indicate a good fit whereas a stress value greater than 0.3 is no better than arbitrary (Clarke 1993). The Bray-Curtis distance measure was used to determine similarities between sites, after loge + 1 transformation of coded abundance data, which was used to down weight the effect of numerically dominant taxa and take greater account of taxa diversity.

To determine the significance of invertebrate community differences an analysis of similarities (ANOSIM) was performed in PRIMER (Clarke and Warwick 1994). Pairwise R values give an absolute measure of how separate groups are on a scale of 0 (indistinguishable) to 1 (all similarities within groups are less than any similarity between groups)

Spring sites 18, 34, 41 and 42 (Figure 1, Appendix 1 & 2) were removed from the assessment of functional feeding groups (FFG) and diversity across sites, due to intermittent connections with the main channel and hill slope streams. These sites were retained for the Nmds in order to encompass the full range of habitat types.

3.3 Results

3.3.1 Continuous stage height and temperature monitoring

Over the six months between June and December 2004 continuous hydrographs of springs (sites 1, 3, 6 and 7), a hill slope stream (Turkey fan) and the main channel (regional council data) were marked by a number of distinct peaks which coincided with the occurrence of westerly air flows over the Southern Alps and “Nor west” rain (Figure 3). However, the relative response of each stream type was different. The hill slope streams showed the greatest variation in relative discharge. Concurrently, regional council data showed that the Waimakariri River followed a similar pattern, but barely responded to smaller falls of rain that created peaks in the hill slope hydrograph. In contrast, the springs did not respond to minor events but, did respond when there were large peaks in the Waimakariri River hydrograph. Relative discharge in springs appeared to be more closely linked to patterns shown by the

Waimakariri River than hill slope streams, however, changes in relative discharge were gradual and less pronounced.

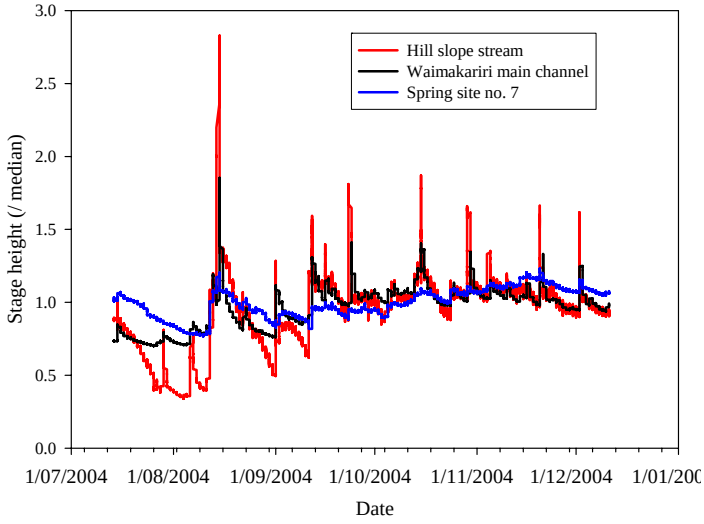

Figure 3. Stage height (standardised to the median value) compared between a hill slope stream, spring and the Waimakariri River.

Temperature fluctuations within the spring site during July and August were minimal (<2^{o}C), and corresponded to changes in air temperature (Figure 4). The hill slope stream was consistently cooler in the winter months, but also showed a more pronounced reaction to changes in air temperature. Over the entire 6 month period, temperature within the spring fluctuated by 1.6^{o}C, whereas the hill slope stream exhibited a range of 8.5^{o}C and air temperature ranged over 35.4^{o}C.

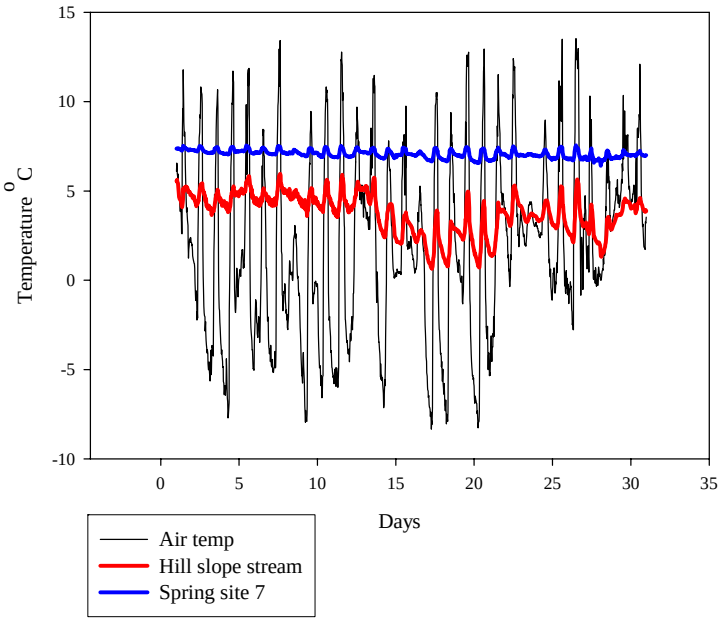

Figure 4. Spring and hill slope stream water temperatures compared to air temperature over a 30 day period during July/August 2004.

Hydrographs for four spring sites with different discharge regimes illustrate the extent of flow variation that occurred within springs (Figure 5). An ephemeral spring (site 6) was dry for long periods of time (Figure 6b). However, during wet periods relative discharge within the spring was very close to that of the permanent spring-fed habitats. In contrast, the source of site 1 is an area of marshy ground and it also received occasional water from an intermittent hill slope stream (Figure 6a). The addition of surface-water resulted in a pronounced spike in this site's hydrograph, however, in the absence of a hill slope subsidy relative discharge is again similar to that in the stable spring (site 7) (Figure 6c). Site 3 also received water and considerable amounts of silt from an intermittently flowing surface-fed stream. Peaks in the hydrograph were due to flooding of the surface-fed stream, and the steady rise in the level of relative discharge to the accumulation of large quantities of silt in the

stream bed. Although all these sites are predominantly groundwater-fed they showed varying degrees of permanence and influence from surface run-off.

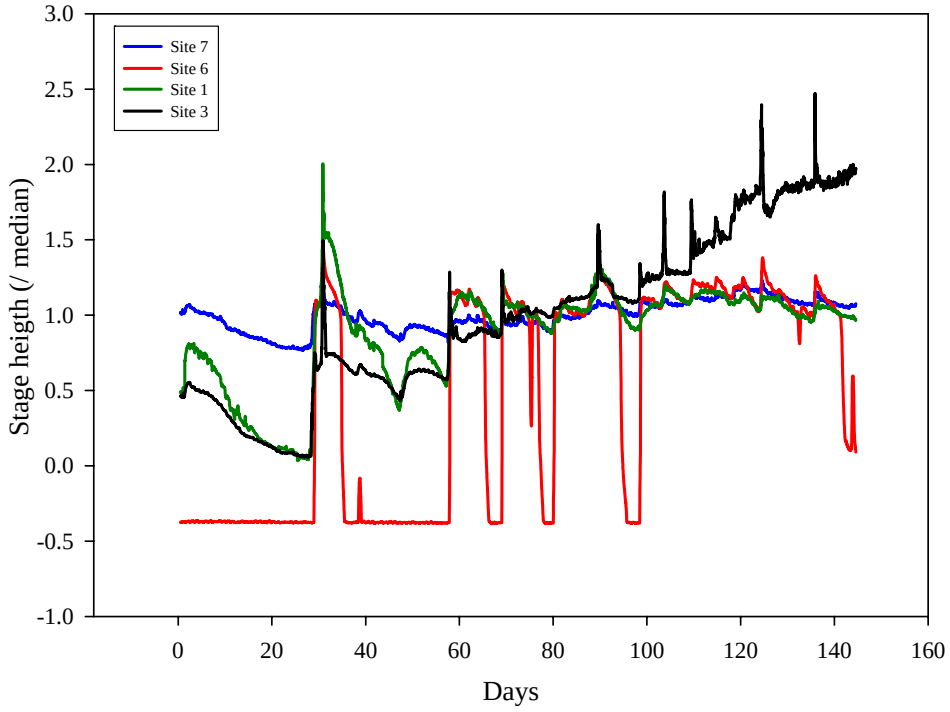

Figure 5. Comparison of standardised stage height between four spring habitats with contrasting discharge regimes over a period of 140 days between July and December 2004.

A) Site 1, showing outflow of pond (channels to left) and the source of intermittant surface flow (stream bed in background)

B) Site 6, at low flow

C) Site 7, Stable discharge and temperature spring

Figure 6. Three of the spring sites monitored by stage height recorders over a six month period.

The four spring sites also showed marked differences in temperature (Figure 7). The ephemeral site recorder (site 6) logged air temperature during dry periods, however, during peak discharge around day 30 (Figure 5) the site was wet and temperatures corresponded closely with those of the stable spring (site 7). As site 6 began to dry up, and flow ceased, diel temperature fluctuations increased until once again air temperature was recorded. During the dry period prior to day 30, diel fluctuations were pronounced at both sites 1 and 3, but after a rise in the water table levels, temperatures of both sites approached that at site 7. This suggests that ponding and consequent temperature regulation of spring water, by solar irradiance and ambient air temperatures, occurred during low discharge periods.

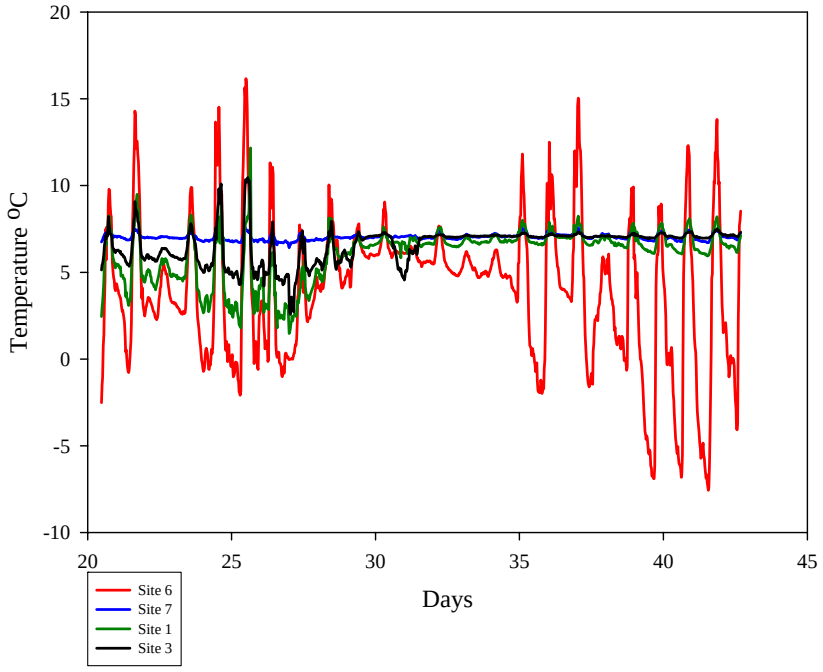

Figure 7. Temperature variation at four spring-fed sites over 25 days in August 2004. The days marked on the X axis correspond to the scale in figure 5.

3.3.2 Physicochemical habitat variables

Discharge in the main channel was at least three orders of magnitude greater than in either springs or hill slope streams, and hill slope streams were also significantly smaller than springs (Table 1). Disturbance intensity, as measured by particle movement, was significantly greater in main channels than spring sites, although some variation did occur among the springs.

Table 1. Comparisons of mean habitat variables between spring, hill slope and main channel habitats in the Waimakariri River. Tests for differences in macrophyte % cover do not include the Waimakariri River which was devoid of plants. Significant *p* values are in bold. NA = not available.

Variable	Springs (n = 42) Mean (± 1 SE)	Hill slope (n = 7) Mean (± 1 SE)	Main channel (n = 7) Mean (± 1 SE)	*p*
Discharge (m^3s^{-1})	0.21(0.03)	0.024 (0.01)	155.4 (0.33)	< **0.000**
Disturbance (%)	4.5 (1.49)	NA	98.9 (0.74)	< **0.000**
Substrate (SI)	4.27 (0.1)	4.46 (0.18)	4.60 (0.06)	0.568
Conductivity (µs cm^{-1} 25°C)	61 (2.40)	108.75 (9.74)	54.57 (2.78)	**0.001**
Macrophytes (%)	16 (2.40)	0	0	< **0.000**
Moss (%)	10 (2.55)	14.5 (8.57)	0	0.443
Algae (%)	18 (2.85)	3.5 (2.36)	0	**0.020**
Total plants (%)	44 (4.88)	18.14 (10.6)	0	**0.032**

Substrate size (SI) did not differ among habitat types, although both spring and hill slope sites were highly variable and some springs showed high levels of silt. Tukey's post-hoc test indicated that whereas mean conductivity in springs and main channel sites did not differ, it was higher in hill slope streams. Macrophytes, mosses and filamentous algae were not observed in the main channel. Percentage moss cover was similar in springs and hill slope streams, but springs had significantly more macrophytes, algae and total plant cover.

3.3.3 Invertebrate community composition of habitat types

Ordination of sites using $\log_e$ semi quantitative coded abundance data was performed to assess similarities between habitats in terms of community composition (Figure 8). The ordination shows that the three habitats have different communities of invertebrates.

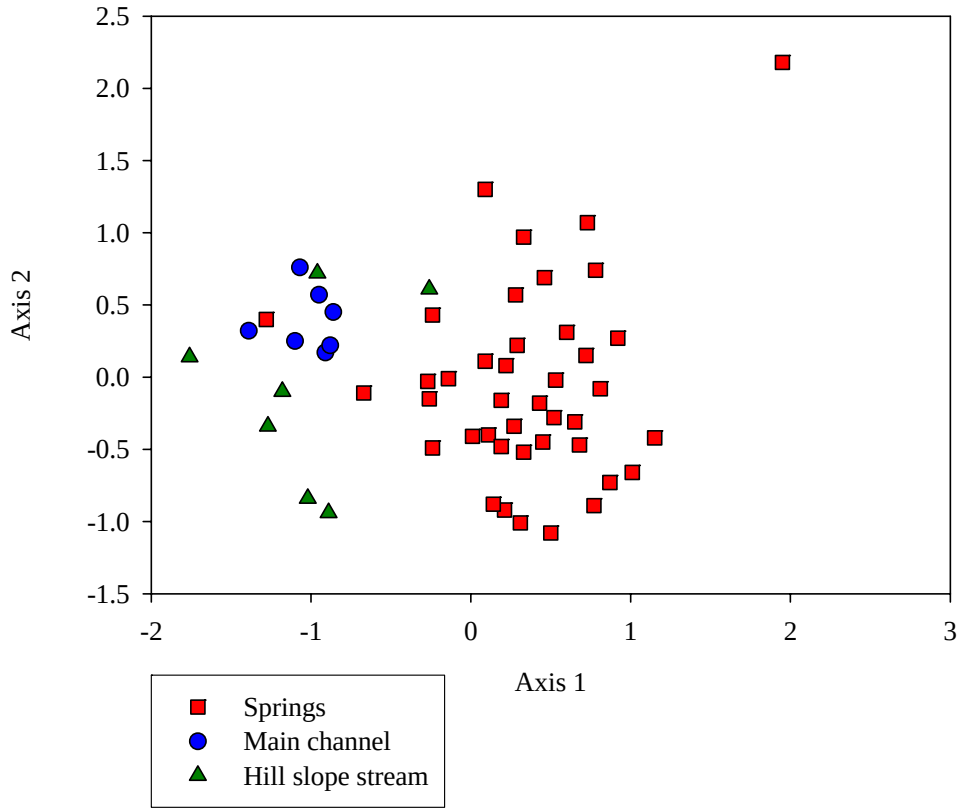

Figure 8. Ordination of spring, hill slope and main channel sites using log abundance data. Stress = 0.18 (n = 55).

Spring sites show a lot of variation in multidimensional space compared to the main channel and hill slope communities. ANOSIM indicated that despite some overlapping of sites invertebrate communities were different overall (global R-statistic = 0.54, $p<0.05$) (Table 2).

Table 2. ANOSIM results testing differences between stream types in terms of benthic invertebrates collected during June and December 2004 Significant results (p<0.05)

Stream types	R-statistic	*p*
Spring – Main channel	0.528	0.001
Spring – Hill Slope	0.618	0.001
Main channel – Hill slope	0.401	0.010

These results indicate that invertebrate communities in springs are highly dissimilar to both main channel and hill slope stream communities. Main channel and hill slope stream communities overlap in composition as suggested by the ordination plot (Figure 8).

A further ANOSIM was performed using only spring sites to look for differences between up-welling locations in the survey. The low global R statistic (0.16) suggested there was little variation between the communities in the seven spring clusters at different locations. Pairwise comparisons indicated some differences between spring cluster invertebrate communities, which might be explained by a greater diversity of spring types in some locations compared to others

Table 3. Significant ANOSIM results for a comparison of spring cluster invertebrate communities. (n = 41, Global R = 0.16). % Significance: <5% = significant.

Spring cluster location	R-statistic	% Sig.
O'Malley's - One tree swamp	0.248	3.2
O'Malley's - Waimak spring	0.518	0.8
Klondyke - Cora Lyn	0.241	1.5
Klondyke - One tree swamp	0.346	1.1
Klondyke - Hawdon valley	0.248	2.6
One tree swamp - Hawdon valley	0.244	2.4
Waimak spring - Hawdon valley	0.424	0.4

3.3.4 Invertebrate community structure

Functional feeding groups (FFGs) were compared between braided river corridor habitat types. The percentage of taxa within each of the FFGs was remarkably similar (Figure 9) despite large differences in the total number of taxa found within each habitat type. Thus, the collector / browser and predator FFGs contained most taxa in

each habitat, however, shredders were absent from the main channel, and piercers were absent from hill slope streams.

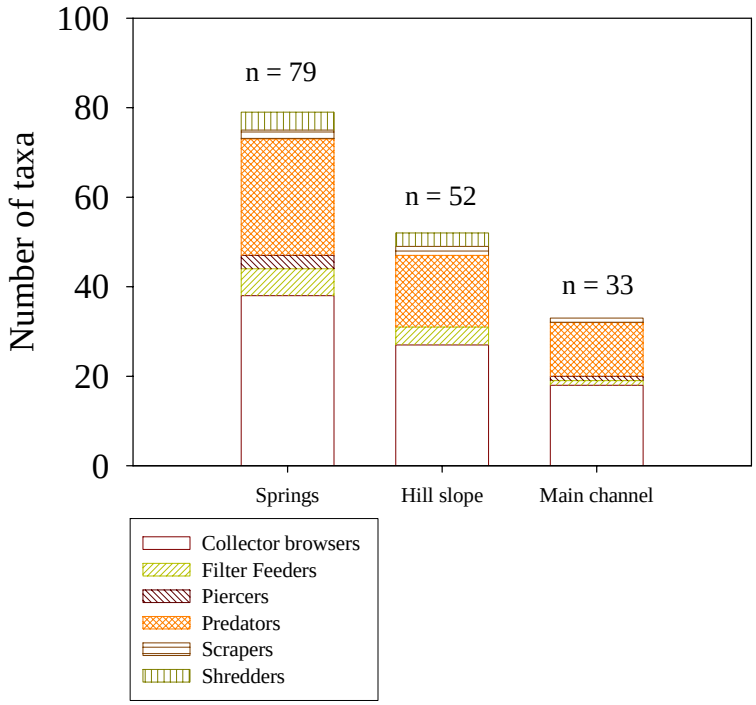

Figure 9. Number of taxa in six functional feeding groups in spring, hill slope and main channel habitats. n = total number of taxa found.

Analysis of relative abundance data from the same sites showed collector/browsers made up 70 to 90% of individuals in all habitats and scraper taxa, predators and filter feeders contributed most of the remainder (Figure 10). The majority of scraper taxa in both springs and hill slope streams were *Potamopyrgus antipodarum*, a hydrobiid snail with cosmopolitan preferences for food and habitats.

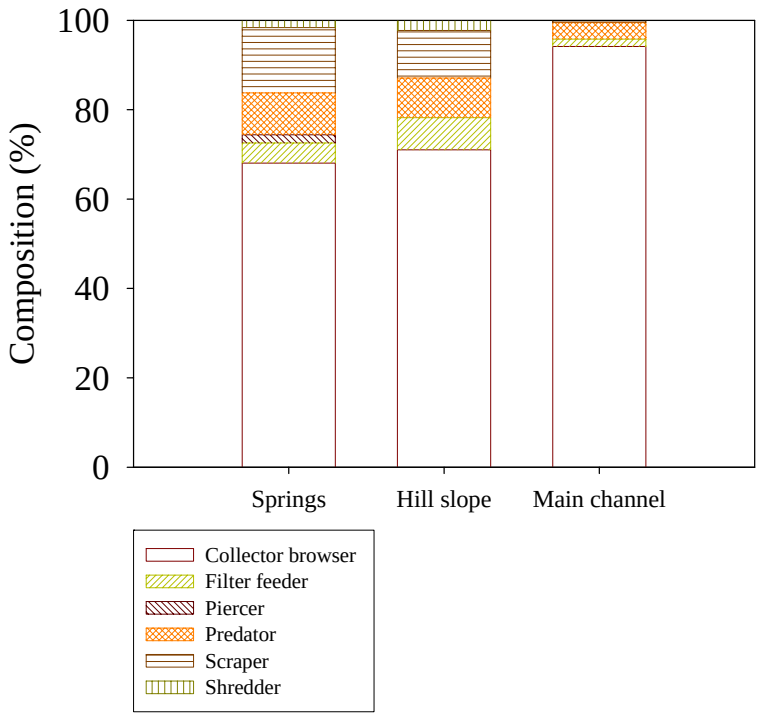

Figure 10. Relative abundance of functional feeding groups within the three braided river habitats.

3.3.5 Diversity across the landscape

Spring sites were taxonomically more diverse (79 taxa) than both hill slope (53) and main channel habitats (33). Approximately 36% of all taxa collected in the Waimakariri River corridor were found only in the springs, compared to 3% in main channels and 13% in hill slope streams. (Figure 11). A group of twenty-two taxa were found at all sites (Table 4). These taxa constituted the majority of taxa found in the main channel, where only three unique types were found. Springs and hill slope streams shared sixteen taxa, and the majority of overall taxa occurred within these habitats.

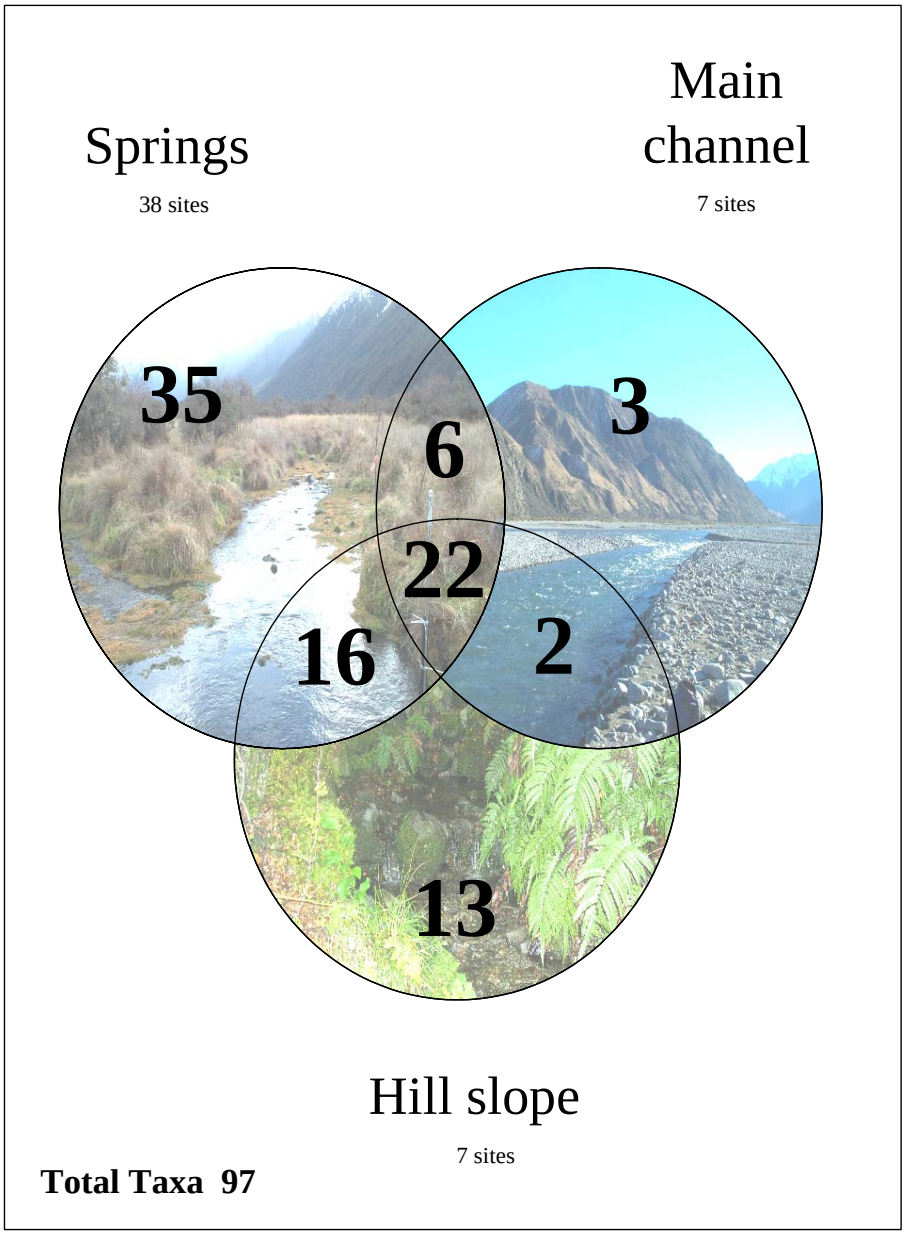

Figure 11. Numbers of taxa unique to spring, main channel and hill slope streams and combinations of the above.

Although there was a sampling effort bias towards springs sites this pattern in taxonomic richness fits with our understanding of the influence of disturbance and stability on New Zealand's benthic invertebrate fauna (Death and Winterbourn 1995, Winterbourn 2004). Furthermore, ANOSIM of spring invertebrate communities (Table 3) revealed little difference between locations suggesting spring faunas were

similar in the different spring complex locations, across the study reach. Overall, these results suggest that the invertebrate taxa found in springs are relatively constant at all locations, thus, high diversity is not the legacy of a sub-set of sites, but indicative of all springs.

Table 4. Taxa found only in spring, hill slope and main channel habitats and combinations of the above.

Springs	Main channel	Hill slope
Nannochorista philpotti	*Hydrobiosis harpidiosa*	*Nesameletus austrinus*
Kempynus sp.	*Hydrobiosis torrentis*	*Austroclima* sp
Megaleptaperla grandis	*Hydrobiosis charadraea*	*Oniscigaster wakefieldi*
Cristaperla sp.		*Hydrobiosella* sp.
Pycnocentria funerea		*Hydrobiosis silvicola* gp
Triplectides obsoletus		*Edpercivalia* sp.
Pycnocentria evecta		*Hydrochorema tenuicaudatum*
Zelolessica cheira		*Hydrobiosis neadelphus*
Paroxyethira eatoni		*Oecetis unicolor*
Hydrobiosis clavigera		*Antiporus femoralis*
Hydrobiosis soror		Hydraenidae
Hydrobiosis chalcodes		Nematomorpha
Polyplectropis sp.		*Archichauliodes diversus*
Philorheithrus agilis		
Hudsonema amabile		
Hudsonema alienium		
Psychodidae		
Limonia sp.		
Zelandotipula sp.		
Stradiomyidae		
Empididae		
Sciomyzidae		
Nothodixa sp.		
Paraleptamphopus sp.		
Oniscoidea		
Ostracod		
Sigara sp.		
Ptilodactylidae		
Huxelhydrus syntheticus		
Antiporus strigosulus		
Liodessus deflectus		
Prorhynchus putealis		
Hirudinaea		
Sphaeriadae		
Lymnaea tomentosa		

Main channel - hill slope	Spring - main channel	Spring - hill slope	Spring - main channel - hill slope
Hydrophilidae	*Nesameletus ornatus*	*Coloburiscus humeralis*	*Deleatidium* spp
Neocurupira spp.	*Pycnocentria evecta*	*Taraperla howsei*	*Stenaperla maclellani*
	Oxyethira sp.	*Austroperla cyrene*	*Zelandoperla* sp.
	Hydrobiosis parumbripennis	*Spaniocerca* sp.	*Zelandobius unicolor*
	Trailochorema sp.	*Zealandobius confusus*	*Zelandobius pilosus*
	Phreatogammarus spp.	*Halticoperla viridans*	*Zelandobius furcillatus*
		Zelandopsyche ingens	Hydrobiosidae indent
		Pycnocentria sylvestris	*Costachorema psaropterum*
		Aoteapsyche colonica	*Psilochorema* sp.
		Olinga feredayi	*Beraeoptera roria*
		Oeconesus maori	*Pycnocentrodes* sp
		Hexatomini	Scirtidae
		Chironominae	Elmidae
		Turbellaria	Muscidae
		Acari	*Aphrophila* sp.
		Potamopyrgus antipodarum	Eriopterini
			Tanypodinae
			Diamesinae
			Orthocladiinae
			Oligochaeta
			Austrosimulium sp.
			Ceratopogonidae

3.4 Discussion

3.4.1 Physical template of river corridor habitats

The three braided river habitats surveyed in this study proved to be physically and chemically dissimilar. The differences were associated primarily with the different sources of water of each habitat. Main channel and hill slope habitats derived water predominantly from rain and snow melt, and discharge was therefore highly responsive to precipitation in the catchment. Conversely, spring habitats appeared to derive much of their flow from groundwater aquifers beneath the flood plain of the braided river. Although ground-water levels were dictated by precipitation in the catchment, they did not show the dramatic fluctuations observed in surface-fed streams. Similar relationships between water table and main channel discharge have been observed in braided rivers in the North America and Europe (Stanford and Ward 1993, Burgherr et al. 2002).

The springs in this study had highly stable substrates, which allowed macrophytes, bryophytes and algae to establish at high densities. Although no disturbance data were collected for hill slope streams they demonstrated erratic discharge levels, with a pattern similar to that observed in the main channel. The presence of aquatic plants is dependant upon flow velocity and substrate stability (Riis and Biggs 2001). Thus, despite fluctuating discharge in hill slope streams the presence of bryophytes suggest that substrate was more stable than in the main channel were no aquatic plants were able to colonise the shifting alluvium. Percentage bryophyte cover was the same in hill slope streams and springs, but cover of filamentous algae was greater in springs possibly because of the increased light levels on the un-forested flood plain (Biggs

and Kilroy 2004). My results concur with the findings of Michaelis (1974) in Waikoropupu Springs, Nelson, where the angiosperms and algae covered a greater area of the spring than bryophytes, due to the combined effects of variation in velocity, substrate type and high light levels. Similarly, Suren (1991) found more algae in unshaded than shaded sites in New Zealand alpine streams whereas, bryophytes occurred on stable substrates at both shaded and unshaded sites.

Temperature regimes were not recorded continuously in the main channel for logistic reasons, however on the six occasions (June to December) that spot measurements were taken the maximum range was 3.4^{o}C, very similar to the results obtained by continuous temperature recording in main channel of the glacial, braided, Val Roseg River in Switzerland, over 1 year (Ward et al. 1999a). The low variability in main channel temperature is thought to be a function of the large size of the river, and its interaction with groundwater. A large river has many sources exhibiting potentially varied temperatures, and due to its large volume to surface area ratio is less responsive to ambient air temperatures (Ross 1963). Hydrological exchange between alluvial aquifers and surface-water also modulate temperature as aquifer water tends towards a constant temperature (Ward et al. 1999a). Temperature variability of the hill slope stream was dependent upon ambient air temperature, although Smith and Lavis (1975) indicate that snow melt and geology can result in discrepancies from this pattern. Within springs, temperatures were very stable when flow was dominated by groundwater although, small fluctuations were observed that corresponded to changes in air temperature. However, when the water table was low temperatures in springs fluctuated more widely. So, although ground-water exhibits stable temperatures,

thermal constancy in springs is regulated by the relative stability of discharge and its degree of permanence, moderated by diel fluctuations in air temperature.

In summary, main channel habitats displayed high levels of substrate instability and discharge variability. Temperatures were relatively stable and the substrate was devoid of aquatic plants. Hill slope streams experienced large fluctuations in discharge, but due to the presence of bryophytes are inferred to have intermediate levels of substrate in-stability. Algal cover was assumed to be low due to shading, and temperature fluctuations high due to the small size of streams and diel changes in air temperature. Springs had stable substrates, discharge and temperature, which allowed an abundant growth of macrophytes, bryophytes and algae, particularly in un-shaded sites.

3.4.2 Invertebrate communities

My results indicate that in terms of taxonomic diversity the three habitats considered were quite distinct. Despite some overlap between habitats and the well documented "generalist core" of taxa found in New Zealand, each habitat contained unique taxa (Winterbourn et al. 1981). Differences between spring communities at each location were minimal, indicating that throughout the entire study reach the distinct communities within springs were relatively constant. Differences in community structure of pristine New Zealand montane streams appear to be related to physical factors, although the presence of fish can affect community structure (McIntosh 2000). Stream size, slope and stability followed by the nature of available energy sources dictated community composition in Devils Creek on the West Coast (Cowie 1980). The streams surveyed in my study exhibited extremes in both the former

physical conditions and energy source, thus, driving the disparities in invertebrate community composition. Winterbourn et al. (1981) argued that whilst highly unstable stream beds may support diverse faunas, the highest diversity is associated with stable habitats exhibiting a high degree of substrate heterogeneity. The results of my study concur with this contention in that the two habitats that experienced the greatest levels of disturbance (main channels and hill slope streams) contained fewer taxa than the stable spring sites. Furthermore, main channel and hill slope habitats showed more commonality in biotic communities possibly due to the predominance of physical drivers over biological ones in filtering local invertebrate communities from the regional species pool (Poff 1997).

3.4.3 Invertebrate community structure

Spring habitats had more diverse invertebrate communities than hill slope streams, which in turn contained more species than the main channel. However, the proportion of taxa within each functional feeding group remained relatively similar across habitat types. Furthermore, the mean relative abundances of functional feeding groups were similar among the three habitat types. Main channel habitats were strongly dominated by collector / browsers, the majority of which were *Deleatidium* larvae. This taxon is highly adapted to the constantly shifting substrate and low food resource levels of the Waimakariri River main channel (Winterbourn 1977, Sagar 1983, 1986, Scrimgeour 1987). In contrast, scrapers were absent from the main channel. Taxa such as the mollusc *Lymnea tomentosa* were found only in springs, the blephariceridd *Neocurupira* in hill slope streams, and *Potamopyrgus antipodarum* was abundant in both habitats. These organisms feed by adhering to substrate surfaces and grazing

periphyton and detritus. P*otamopyrgus* and N*eocurupira* have contrasting adaptations that enable them to cope with high water velocities. The latter is dorso-ventrally flattened, and equipped with powerful suckers to resist rapid flowing currents which are characteristic of its habitat of preference (Craig 1966, Winterbourn et al. 2000, Frutiger 2002). In contrast, *Potamopyrgus*, in experimental channels, responded to high flows by moving rapidly into the deeper sub-layers of substrate (Holomuzki and Biggs 2000). Neither taxon, seems to be able to deal with the moving substrate found in the main channel however, and the numerical dominance of *Potamopyrgus* in both springs and hill slope stream communities reflects its ability to use both allochthonous detrital food resources in the hill slope streams, and autochthonous algal resources in the springs (Dorgelo 1991 cited in Winterbourn 2000). The lack of piercers (*Oxythira* and *Paroxythira*) in hill slope steams and the main channel probably reflects the low level of macrophytes and filamentous algae with which they are associated and their preference for low flow velocities (Leader 1972, Winterbourn et al. 2000).

3.4.4 The contribution of springs to landscape diversity

Natural riverine landscapes are dynamic, and biologically and spatially complex (Ward et al. 2002). Such river landscapes, which include the inter-montane basin of the Waimakariri, may be characterised by extensive flood plains, a natural flow regime (Poff et al. 1997, Young et al. 2004), high hydraulic connectivity, (Brunke and Gonser 1997, Ward et al. 1999b, Woessner 2000), a successional landscape mosaic with high habitat heterogeneity (Arscott et al. 2000, van der Nat et al. 2003) and complex ground-water surface-water exchange (Stanford and Ward 1993, Brunke and Gonser 1997, Poole et al. 2002). The high spatio-temporal habitat heterogeneity created by these conditions supports a diversity of invertebrate taxa across a range of successional landscape stages.

The springs and main channel habitats considered in this study are polar extremes in terms of their physicochemical characteristics, and yet are both part of a single body of water moving along the Waimakariri river flood plain. Hydrological connectivity mediated by the flood plain aquifer, and maintained by flood induced fluvial dynamics, results in stable spring habitats occurring amidst the highly disturbed braided channels (Ward et al. 1999b). These disparate habitats are united as parts of an expanded 3-dimensional view of the "river" within the landscape (Stanford 1998).

My results indicate that hydrological connectivity enhances river corridor invertebrate diversity, and that spring-fed habitats are hotspots of diversity within this landscape. They constitute a stable habitat for invertebrates unable to colonise unstable, flood prone environments, but also an ecotone between surface-waters and groundwater's where a number of phreatic taxa may exist. I found that springs contained more taxa overall than any other habitat, and also the highest number of taxa unique to any one habitat. This finding is in accordance with Barquin's (2004) national comparison of New Zealand spring and surface-fed streams, and other studies that have compared spring and surface-fed braided river systems in New Zealand (Death and Winterbourn 1995, Digby 1999) However, several studies that have compared invertebrate communities in springs and surface–fed streams or downstream reaches in Europe and America have found that diversity was highest in the surface-fed streams (Davidson and Wilding 1943, Ward and Dufford 1979, Anderson and Anderson 1995, Barquin and Death 2004). Such a pattern has been attributed to northern hemisphere spring communities being dominated by a low diversity of predators, and the deleterious effects of thermal constancy upon taxa with seasonally synchronised life-cycles

(Barquin and Death 2004). However, in a braided flood plain reach of the glacial Val Roseg River, Switzerland, Burgherr et al. (2002) found higher taxonomic diversity in groundwater-fed channels than in the main channel. High levels of disturbance found in glacial outwash rivers may result in low main channel diversity, whereas the dynamic nature of braided river flood plains may prevent spring communities from reaching later successional stages where competitive exclusion/predation alter community structure (see chapter 4).

Common, widely distributed invertebrate taxa are often the most abundant in New Zealand streams (Boothroyd 2000). Whereas, a large number of rare species typically make up a small percentage of the total invertebrate abundance within a particular habitat i.e. they are rare (Cowie 1985). Consequently, many of the taxa unique to springs, hill slope streams or the main channel are not only limited in their distribution, but are rare within these habitats.

The high degree of endemicity of benthic invertebrate species in New Zealand, due to its relative isolation and early separation from Gondwana (Boothroyd 2000), means that many of the taxa inhabiting the remaining pristine landscapes are globally unique. Abstraction and degradation of lowland surface and groundwater systems further exacerbate the situation. Enigmatic taxa such as the phreatic amphipods *Phreatogammarus* sp and *Paraleptamphopus* sp, and the flatworm *Prorhynchus putealis*, which have been found historically in the rivers of the Canterbury plains and springs in the Waimakariri inter-montane basin (Percival 1945), are dependant upon the integrity of groundwater systems. Many lowland surface-water habitats are already seriously degraded (Meredith et al. 2003), but our understanding of aquifer

hydrology and ecology is still too limited to understand the impacts of agricultural activities on these subterranean environments. Thus, the intact, relatively pristine braided rivers of the Southern Alps may soon hold the remaining vestiges of some of New Zealand's more unusual benthic communities, and as such represent important and valuable habitats in their entirety. Springs contain the greatest bio-diversity, but need to be seen as a feature of an intact, entire river system, not as isolated entities. Protection of an area of high local diversity therefore, requires a holistic approach to catchment or regional habitat diversity.

3.4 Conclusion

Hill slope, main channel and spring habitats in the upper Waimakariri catchment showed predictably extreme differences in physico-chemical conditions. These differences were reflected by their benthic invertebrate communities in terms of the taxa present. The springs represent hotspots of bio-diversity within the river corridor. They are home to a range of taxa many of which are locally and regionally rare, and globally unique.

4

Patterns in spring benthic invertebrate communities

Photo: Jens Zollhoefer

Prorhynchus putealis Photo: Michelle Greenwood

4.1 Introduction

Within a braided river ecosystem springs exhibit quite different physicochemical characteristics to the two other common freshwater habitats, hill slope streams and main channel environments. As a result, the biological communities of spring-source environments are quite distinct (Chapter 3). However, not all springs are physically or biologically the same and different invertebrate communities have been reported at spring-sources, moving downstream away from the source, and between springs with different disturbance histories (Ward and Dufford 1979, Williams et al. 1997, Hoffsten and Malmqvist 2000, Barquin and Death *in press*).

Several authors have suggested that the primary drivers of communities at spring-sources may be biogeographic, but in-stream conditions such as substrate, flow velocity and water chemistry are also important (Glazier 1991, Williams 1991, Hoffsten and Malmqvist 2000, 2004, Barquin and Death *in press*). All the springs in my study are located within the upper Waimakariri flood plain, and have been subject to the same climatic events, e.g., glaciation. Therefore, I have been able to examine the role of in-stream conditions, on the structuring of macro-invertebrate communities, in the absence of biogeographic or regional variation.

In Europe and North America several studies have demonstrated a longitudinal pattern of increasing benthic invertebrate diversity downstream from a spring source (Sloan 1956, Minshall 1968). Two main theories have been advanced explain this trend. Firstly, it might be the result of sub-optimal physicochemical conditions at the spring-source, affecting the growth, reproduction and life cycles of benthic invertebrates (Ward and Dufford 1979). Secondly, competitive exclusion may occur

between species, due to high environmental stability at the source, whereas downstream the greater instability creates more ecological niches and competition is reduced (Sloan 1956, Minshall 1968, Barquin 2004). In New Zealand however, a contrasting pattern of high invertebrate diversity at more stable sites has been observed by Death (1991), although it is important to note that his comparisons were made between spring-fed and non-spring-fed streams. Attempts to explain this contrary trend in New Zealand have found that whereas springs have higher invertebrate diversity than less stable hill slope streams, stable spring-sources were less diverse than their downstream reaches (Barquin 2004). Barquin found that diversity and abundance increased away from the source and suggested that this was possibly due to changes in substrate composition, stability, and invertebrate drift.

Spring communities in Europe switch from non-insect to insect dominated communities with an increase in altitude and distance north of the equator (Hoffsten and Malmqvist 2000, Barquin and Death 2004). This was attributed to the time since a major disturbance of springs within the different regions. Milner (2000) found that younger streams communities, over a 200 year gradient in Glacier Bay National Park, Alaska, were more strongly dominated by insects than older streams and attributed this to the different rates of post glaciation dispersal and colonisation by insect and non-insect taxa. Rapidly dispersing insects colonise springs first by virtue of the terrestrial, aerial stage of their life cycle. However, all life stages of non-insect taxa are often restricted to aquatic environments and must therefore disperse through the water, resulting in slower rates of colonisation into new habitats. Therefore, time since a major disturbance may contribute to the benthic invertebrate structure of spring communities.

The primary objectives of the research discussed in this chapter were:

1. To determine the effect of in-stream physicochemical characteristics on the biological communities at spring sources.

2. To assess changes in physicochemical conditions, downstream from the spring-source, and investigate how they affect benthic communities.

3. To examine the effect of site age or time since a major disturbance, on invertebrate communities.

4.2 Method

Data used for these analyses are a subset of the data described in Chapter Three. The methods of physicochemical and biological data collection are the same, except for site age, which was estimated using floristic and alluvium depositional characteristics as outlined by Reinfelds and Nanson (1993) (Table 1). Five categories are recognised ranging from 0 to >350 years.

Table 1. Age brackets for flood plain elements from Reinfelds and Nanson (1993).

Stage 1	Active river bed frequently reworked
Stage 2	3-30 years
Stage 3	30-50 years
Stage 4	50-150 years
Stage 5	100-350 years
Terrace	> 350 years

4.2.1 Data treatment and statistical analysis

It was decided *a priori* to consider stream size and stability separately following Taylor and Warren (2001). Physical variables representing stream size and stream stability were analysed using Principal Components Analysis (PCA) in Systat v10 (2000) to reduce the number of variables and auto correlates.

Variables indicating stream size included mean and maximum width, depth and discharge. Data were log transformed and normalised prior to collapsing the data-set into a single principal component representing stream size.

Stream stability was analysed using measures of substrate disturbance, maximum water velocity and permanence, as well as coefficients of variation for temperature, discharge and conductivity. Substrate disturbance was represented by intensity (the mean percentage movement of painted rocks within two size classes between sampling dates), and maximum bed movement (Bmmax, the maximum recorded movement of stones within a site across all sampling occasions) after Townsend et al. (1997). Percentage permanence of water was calculated as the percentage of sampling occasions when the site had flowing water.

Following ordination of stream size, axis 1 explained 70.1% of the variation in the data set (Table 2), and is used as the index of stream size. In contrast, the stream stability PCA produced axes 1 and 2, which explained 36.9% and 22.8% of the variance, respectively. Measures of substrate disturbance and discharge variability had the strongest relationships with axis 1 which formed an index referred to as stream disturbance (PCA 1). %permanence, max velocity and the coefficient of variation of temperature had the strongest relationships with axis 2, which provided an index of stream permanence (PCA 2).

Table 2. Component loadings and percent variation explained by Principal Components Analysis of variables representing stream size and stream stability.

Stream size		Stream stability		
Size variable	Axis 1	Stability variables	Axis 1	Axis 2
Mean discharge	0.948	Temperature (CV)	0.533	-0.551
Mean width	0.885	Discharge (CV)	0.727	-0.266
Max discharge	0.873	Conductivity (CV)	0.137	-0.361
Max width	0.856	Disturbance intensity	0.823	0.379
Mean depth	0.723	BMMAX	0.836	0.398
Max depth	0.71	Max velocity	-0.411	0.532
		% Permanence	0.137	0.717
Variance explained	70.1%		36.9%	22.8%

Non-metric multi dimensional scaling (Nmds) using the Bray-Curtis similarity measure, of spring-source sites was performed to examine patterns in community composition using the PRIMER v5 statistical package (Clarke and Warwick 1994). Relationships between Nmds axis scores and their component invertebrate taxa data were assessed using Spearman's rank correlation coefficient, whilst patterns between Nmds axis scores and physicochemical variables were investigated using simple linear regression in Systat v10 (2000).

To test for differences between physicochemical conditions at spring-source and downstream spring brook sites, Mann-Whitney U tests were performed using Systat v10 (2000). To examine changes in invertebrate communities with increasing distance from the spring-source, PRIMER v5 (Clarke and Warwick 1994) was used to calculate a range of indices of diversity within each site. Total number of taxa (S), Margalef's index and rarified values represent species richness.

Margalef's index = $D = (S - 1)/\ln N$ Equ. 4.1

where S = number of taxa

N = the number of individuals

Rarefied diversity values are preferable to taxa numbers for comparing habitats when either sample sizes differ, or habitats contain different densities of individuals (Magurran 1988). Rarefaction calculates the number of species that would be expected from samples of a standard size, or with a particular standardised abundance (Magurran 1988). Conventionally, the lowest number of individuals at any site is used to correct the rarefied diversity value. However, in my study one site contained only 11 individuals resulting in a considerable loss of information, so the mean abundance of all sites (113) was used).

$$E(S) = \sum \left\{ 1 - \left[\left(\frac{N - N\mathrm{i}}{n} \right) \Big/ \left(\frac{N}{n} \right) \right] \right\} \qquad \text{Equ. 4.2}$$

Where E(S) = the expected number of taxa in the rarefied sample

n = standardized sample size

N = the total number of individuals recorded in the sample to be rarefied

N_i = the number of individuals in the ith species in the sample to be rarefied

Total number of individuals (N), Shannon's index of evenness and Simpson's index of dominance were also calculated in PRIMER v5 (Clarke and Warwick 1994).

Shannon's diversity index: $H' = \sum Pi \ln Pi$ Equ.4.3

Where Pi = the proportional abundance of the ith species = $\left(n_i / N\right)$

Shannon evenness index = $H' / \ln S$ Equ 4.4

Where S = the total number of taxa

Simpson's index of dominance: $D = \sum \frac{\left(n_i\left(n_i - 1\right)\right)}{N\left(N - 1\right)}$ Equ. 4.5

Where n_i = $_{\text{the}}$ number of individuals in the ith species

N = the total number of individuals

It is important to note that a larger Simpson's diversity index indicates lower diversity. Thus, the reciprocal (1-diversity) was taken so that the value of the index increased with increasing diversity.

The relationships between these biotic indices and distance from a spring-source were examined using simple linear regression in Systat v10 (2000). The relative abundances of six functional feeding groups in both spring-source and spring brooks were investigated, and compared using Mann-Whitney U tests. Changes in functional feeding groups relative to specific "distance from the source" were examined by using Spearman's ranked correlation using Systat v10 (2000).

To assess the relationship between site age and %taxa dominance simple linear regression was performed in Systat v10 (2000).

Site's 18, 34, 41 and 42 were connected intermittently with the main channel and hill slope streams. Thus, these sites were excluded from spring-source analyses. Sites 36 and 6 were also excluded from the analyses of longitudinal change. The source of site 36 was indeterminate (sampling took place in both a spring brook and an adjacent spring source habitat), whilst site 6 was highly ephemeral and often exhibited no flow. All the above sites were also excluded from analyses of taxa dominance and site age.

4.3 Results

4.3.1 Determining spring-sources

The most frequently used delineation for the longitudinal extent of a spring-source is the lower boundary of the eucrenal zone, i.e. the point at which the fluctuation in temperature is greater than 2^{o}C. Spring-source habitats should also be characterised by low physical disturbance and small fluctuations in discharge. Accordingly, I considered the influence of distance from spring-source upon these variables in order to select a sub-set of springs which could be classified as "spring-source" habitats (Figure 1).

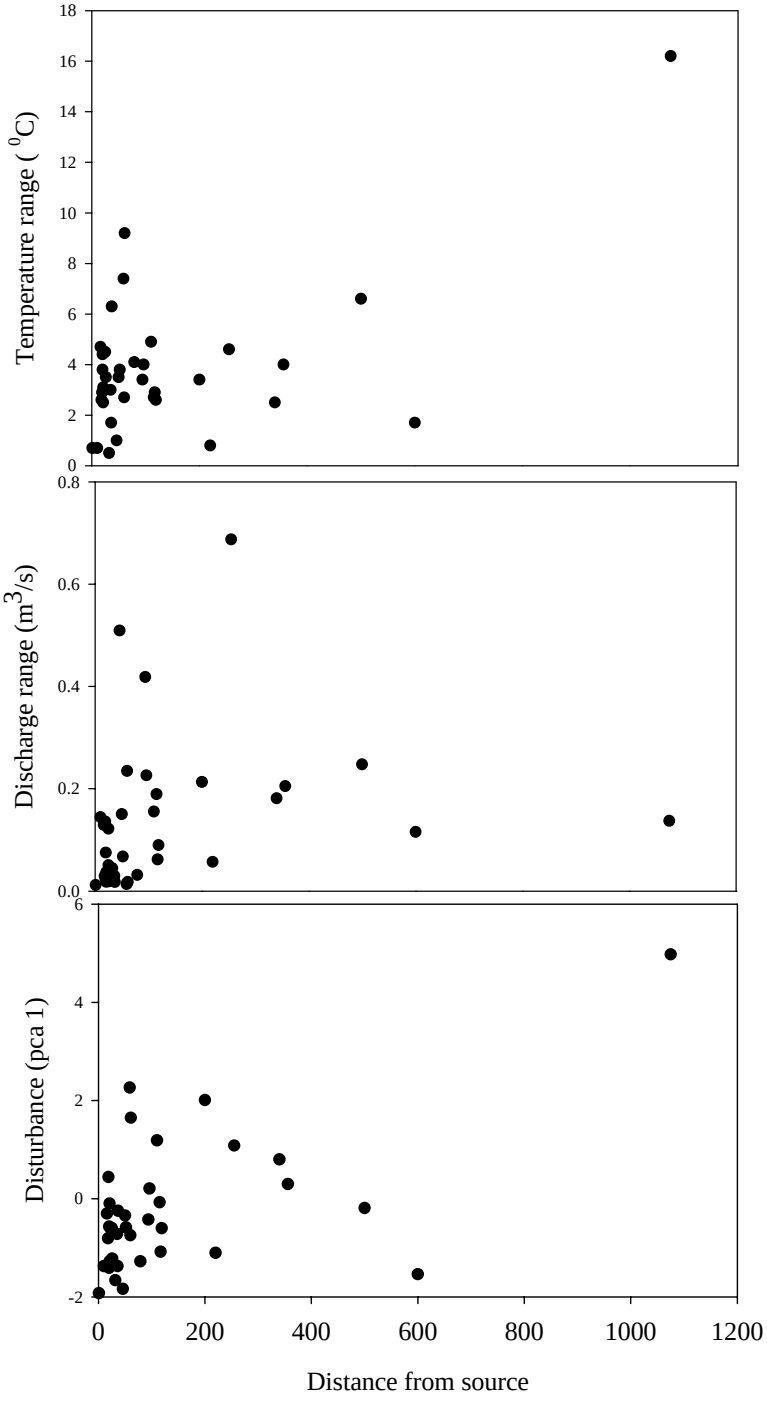

Figure 1. Relationships between distance from spring-source and temperature range, discharge range and the PCA axis representing disturbance within streams (n=36).

Weak relationships were found between distance, disturbance (composite PCA variable), discharge range and temperature range. All three variables showed a

significant regression, however, when distance was log transformed to correct for non-normality (disturbance r^2= 0.266, p=0.001, discharge range r^2=0.16, p=0.01, temperature range r^2=0.16, p=0.01). This analysis also showed that within the first 50 m of springs, temperature, discharge and disturbance within springs were highly variable. Therefore, for these braided river springs, thermal constancy, low discharge range and low levels of disturbance were considered to be unreliable indicators of spring-source conditions. Thus, I decided to use a simple "distance from source" measure of 40 m to define a spring-source. A review of the literature revealed that a number of different distances have been used to define the downstream limit of a spring-source (Table 3), which is not surprising considering the differing hydro-geological contexts within which the studies took place.

Table 3. Distances used in the literature to define a spring-source.

Distance to source	Spring types	Author
10m	Rheocrene	(Erman 1998)
20m	Rheocrene	(Glazier 1991)
25m	Rheocrene/Limnocrenes	(Zollhoefer et al. 2000)
50m	Alluvial and Karst Rheocrene	(Barquin and Death *in press*)
100m	Glaciofluvial, moraine and Karst Rheocrenes	(Hoffsten and Malmqvist 2000)

Sixteen of my sites were therefore classified as spring-sources, two of which are illustrated by Figure 2.

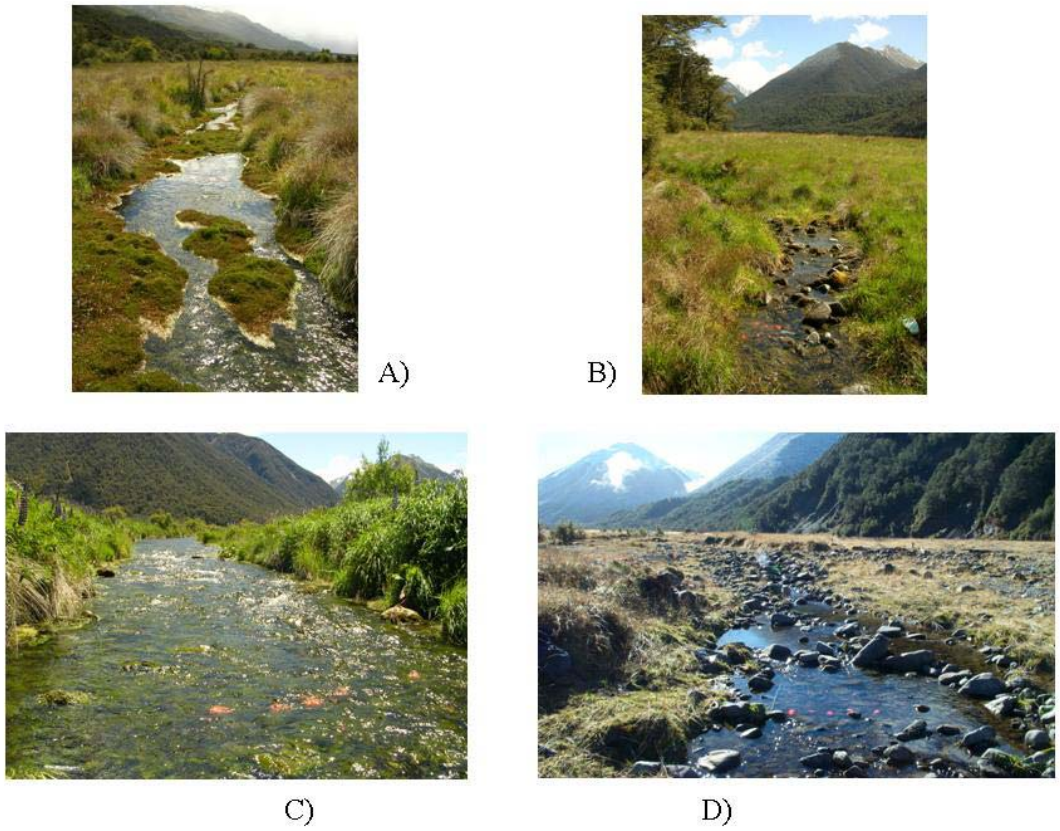

Figure 2. A, B, spring-source habitats at the Turkey fan and Hawdon valley, respectively. Both sites were estimated to be 100 to 350 years old. C, D, spring brooks at Klondyke and in the Hawdon valley. Site C was estimated to be 50 to 100 years old (time since last major disturbance) and site D to be 3 to 30 years old

4.3.2 Physicochemical characteristics of spring-source habitats

Spring-source sites were characterised by a low discharge range and high aquatic plant cover. However, there was considerable variation in the range of temperatures within sites. (Table 4).

Table 4. Physicochemical characteristics of 16 spring-sources.

Temperature (^{o}C)	Mean (SD)	7.8 (1.09)
	Range within springs	0.5 -6.3
Conductivity (µs cm^{-1} 25^{o}C)	Mean (SD)	61.8 (11.41)
	Range within springs	2.6 – 34.9
Discharge (m^3s^{-1})	Mean (SD)	0.04 (0.022)
	Range within springs	0.1 - 0.01
Substrate (cm)	Mean (SD)	4.3 (0.54)
% Silt	Mean (SD)	10.8 (12.33)
Disturbance intensity % (move.)	Mean (SD)	2.03 (2.617)
Slope (^{o})	Mean (SD)	0.6 (0.51)
Macrophyte cover (%)	Mean (SD)	30.8 (26.93)
Algal cover (%)	Mean (SD)	25.6 (20.40)
Plant cover (%)	Mean (SD)	56.4 (31.88)

4.3.3 Spring-source community structure

Non-metric multidimensional scaling of the 16 spring-source sites based on absolute abundance data produced a two dimensional solution with a stress of 0.18 (Figure 3) Axis 1 was significantly correlated ($p > 0.05$) with %Ephemeroptera (r_s crit = 0.503, $p<0.05$, 0.613), %Trichoptera (0.689), %Coleoptera (0.620) and %Diptera (-0.715). Axis 2 was correlated most strongly with the abundance of Ephemeroptera (-0.532). These results indicate that axis 1 is associated with an inverse relationship between the relative abundance of mayflies, caddis and beetles, compared to that of dipterans.

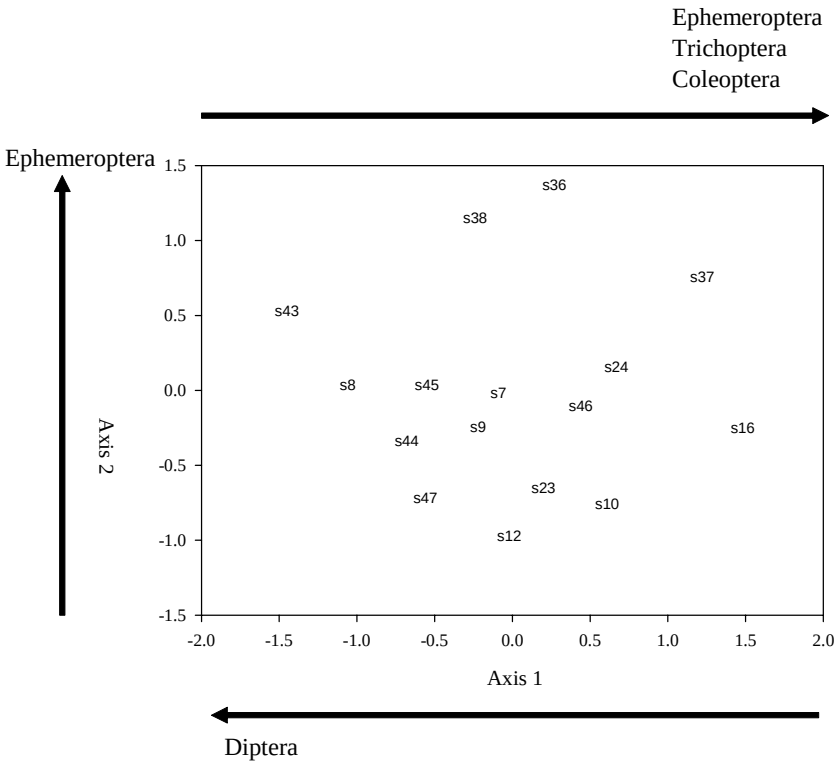

Figure 3. Non-metric multidimensional scaling of spring-source sites (n=16) based on coded abundance of invertebrate taxa. Stress = 0.18. Arrows indicate the direction of correlation between taxa orders and axis scores.

Physicochemical characteristics were regressed against axes 1 and 2 of the Nmds ordination (Figure 4). Axis 1 showed significant relationships with total macrophyte cover, total plant cover, mean temperature, and slope, whereas axis 2 was related to temperature range, stream size, stream disturbance and discharge range.

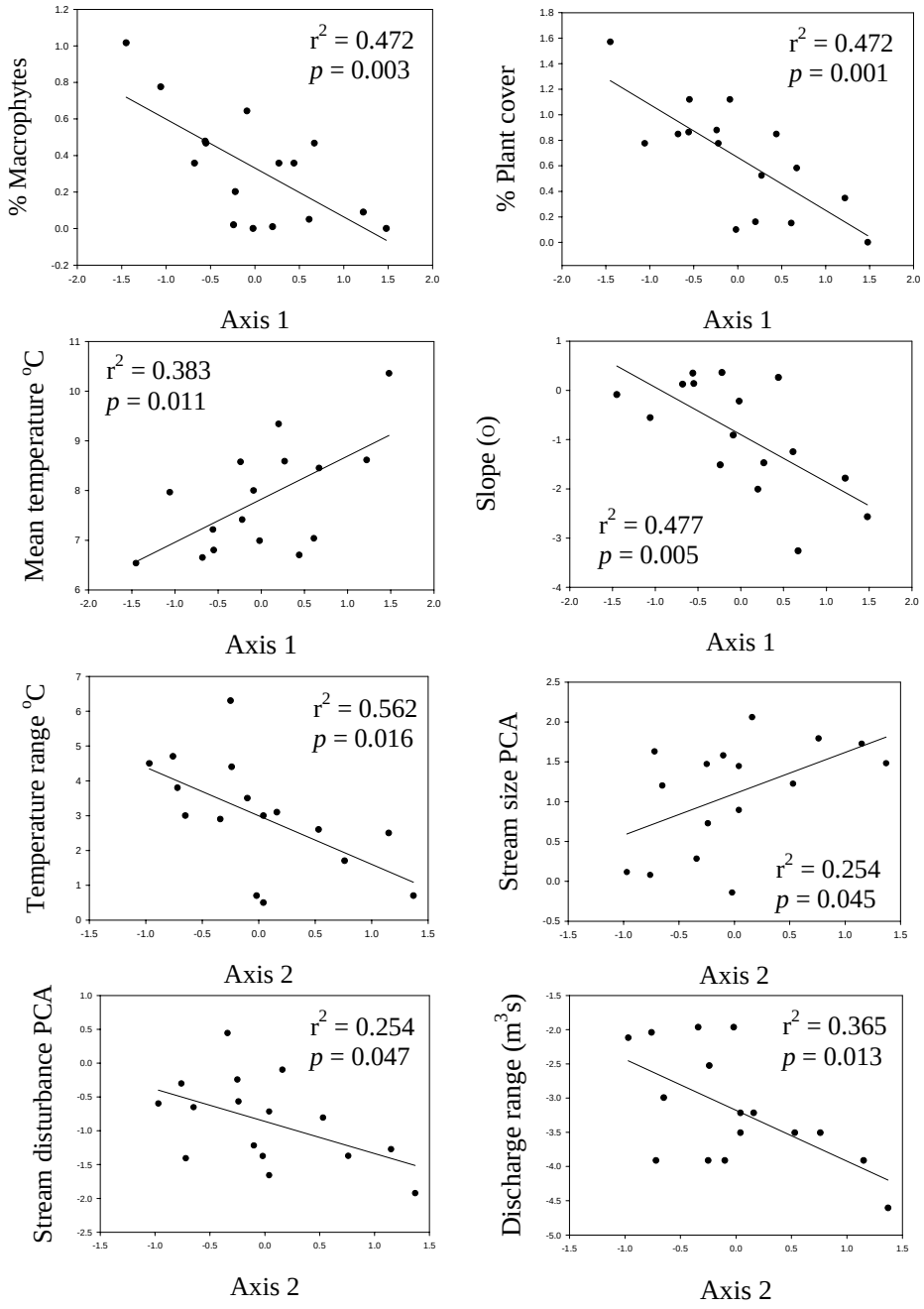

Figure 4. Linear regression of physicochemical variables measured in spring-source sites against axes 1 and 2 of the Nmds ordination.

4.3.4 Longitudinal changes in spring habitat conditions

Temperature ranged from 6.5°C – 10.3°C across all sites, but differed significantly between spring-source and spring brook sites (Table 5). Spring brooks were approximately 1°C warmer than source sites during the six month study period. Although conductivity did not differ between sites, spring brook sites had a wider range of values, than source-sites. Discharge and discharge variability were significantly greater in spring brooks, reflecting the larger potential catchment and more varied sources of water further down the stream. Conversely, the percentage cover of filamentous algae and all aquatic plants (macrophytes, bryophytes and algae) was greater at source than brook sites. Some spring-source sites had 100% plant cover.

Table 5. Physicochemical characteristics of 16 source and 22 spring brook sites. Means (Standard Deviation) are calculated from site means measured over six occasions. Significant *p* values (*p*=>0.05) are given in bold for comparisons of source and brook sites by Mann-Whitney U tests.

		Spring-source	Spring-brook	*p*
Temperature (°C)	Mean	7.8 (1.09)	8.6 (1.22)	**0.026**
	Range within springs	0.5 -6.3	0.8 – 16.4	0.070
Conductivity (µs cm^{-1} 25°C)	Mean	61.8 (11.41)	62.1 (19.59)	0.370
	Range within springs	2.6 – 34.9	1.6 – 69.6	**0.000**
Discharge (m^3s^{-1})	Mean	0.04 (0.022)	0.15 (0.147)	**0.000**
	Range within springs	0.1 - 0.01	0.9 - 0.01	**0.002**
Substrate (cm)	Mean	4.3 (0.545)	4.2 (0.834)	0.789
% Silt	Mean	10.8 (12.33)	16.4 (29.54)	0.847
Disturbance intensity (%)	Mean	2.03 (1.617)	12.4 (17.66)	0.080
Slope (°)	Mean	0.6 (0.513)	0.5 (0.379)	0.850
Macrophyte cover (%)	Mean	30.8 (26.93)	13 (27.67)	0.277
Algal cover (%)	Mean	25.6 (20.40)	10 (16.06)	**0.028**
Total plant cover (%)	Mean	56.4 (31.88)	35.2 (29.59)	**0.039**

4.3.5 Longitudinal changes in invertebrate diversity

Biotic indices describing invertebrate species richness (S, rarified, Margalef's), abundance (N), evenness (Shannon) and dominance (Simpson) were compared in relation to distance from the spring-source (Figure 5). Only the species richness indices had significant, though weak, regressions with distance, and they showed that richness declined away from the spring-source.

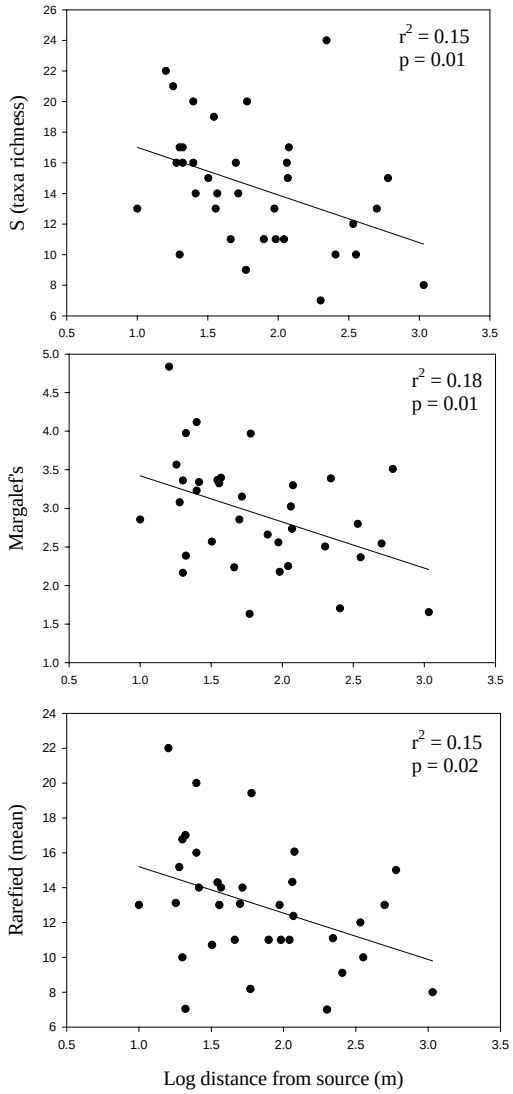

Figure 5. The relationship between three species richness indices and distance from the spring source (n=35).

4.3.6 Functional feeding groups

Across spring-source sites, collector/browsers were the most abundant functional feeding group (FFG) (Table 6). Predators were the second most abundant group, whereas scrapers, shredders, filterers and piercers were poorly represented. Within spring brook sites, a similar pattern was found, except that predators were less abundant and filter feeding taxa were more abundant.

Table 6. Total number of taxa and mean (SD) % abundance of six functional feeding groups at spring-source and spring brook sites. *P* values are for MannWhitney U test's comparing percentages of the two groups. Significant values (p<0.05) are in bold. CB = collector/ browser, P = predator, SC = scraper, F = filterer, Pi = piercer, SH = shredder.

	Spring source		Spring brooks			
	Taxa no.	Mean % abundance (SD)	Taxa no.	Mean % abundance (SD)	Taxa p	Abundance p
CB	27	67 (19.14)	28	67 (19.61)	0.217	0.621
P	18	16 (8.08)	16	13 (12.55)	**0.022**	**0.037**
SC	2	9 (13.23)	2	7 (12.54)	0.227	0.297
F	2	4 (12.87)	6	10 (8.03)	**0.007**	**0.017**
Pi	3	2 (5.22)	2	2 (3.44)	0.930	0.778
SH	4	1 (3.18)	2	2 (1.94)	0.071	0.404

Representation of FFGs was also compared with distance from the source using Spearman rank correlation. Abundance of Collector/browsers, piercers, scrapers and shredders showed no consistent pattern over the maximum of 1 km distance. Downstream however, the abundance of filter feeders increased away from the source (Figure 6a) and the abundance of predators decreased (Figure 6b). Similarly, the percentage of filter feeding taxa increased (Figure 6c), whereas the percentage of predator taxa declined away from the source (Figure 6d).

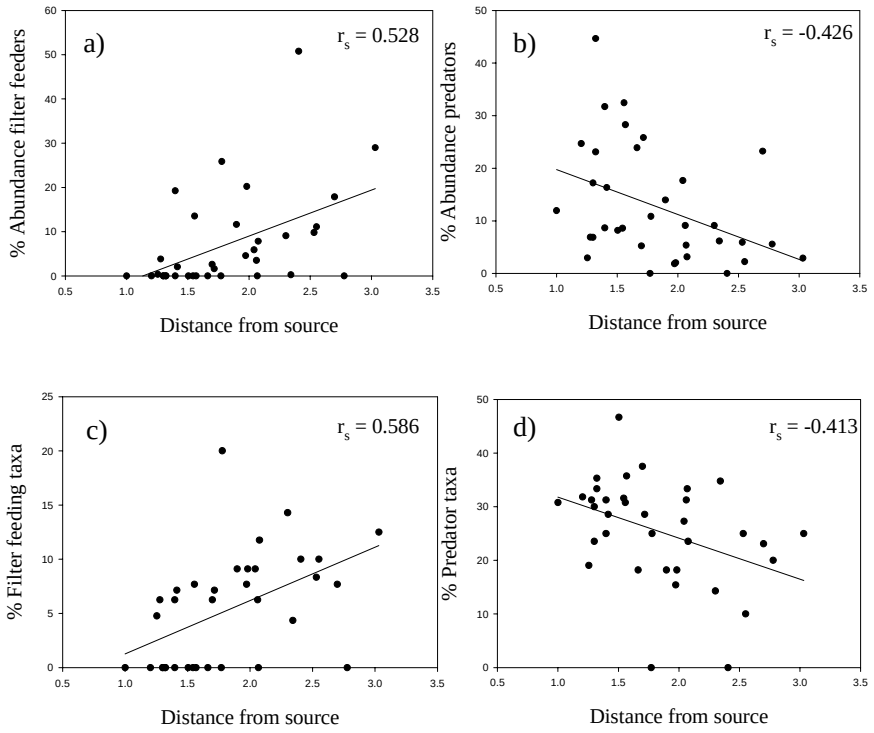

Figure 6. Relationships between functional feeding groups and log_e distance from the spring-source. a) relative abundance of filter feeders, b) relative abundance of predators, c) % filter feeding taxa, d) % predatory taxa.

4.3.7 Site age and invertebrate communities

A total of 65 taxa were identified across all spring-source and brook sites, 58 of which were insects and 10 were non-insects. The most abundant taxa across all sites were orthoclad chironomids, cased caddis *Pycnocentrodes*, and the leptophlebiid mayfly *Deleatidium*. These three taxa also occurred at the greatest number of sites, 94%, 94% and 88%, respectively. In terms of ordinal richness, Trichoptera (24 taxa), Diptera (16), and Plecoptera (8) dominated the insect fauna. Only three Ephemeroptera taxa were collected, *Deleatidium*, *Nesameletus ornatus* and *Coloburiscus humeralis*. Coleoptera were represented by five taxa. The non-insects consisted of three molluscs, three crustaceans, two flatworms, and oligochaete worms.

A significant negative relationship was found between site age and the percentage of insect taxa (r^2 = -0.312, p = <0.001). Thus, younger sites contained proportionately more insect taxa than older sites. (Figure 7). Figure 2 illustrates spring habitats of varying age that were included in this survey.

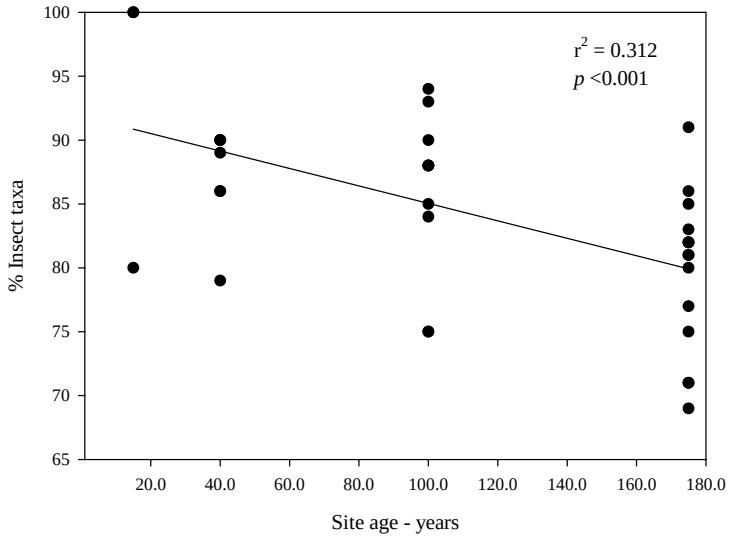

Figure 7. The relationship between site age and percentage insect taxa from 35 sites.

4.4 Discussion

4.4.1 Spring-source communities

Spring-source habitats were typically cool, weedy streams with stable discharge and conductivity. They were dominated by insect taxa, the majority of which feed by collecting and browsing. The ordination of spring-sources indicated there were differences between sites in terms of invertebrate communities and that taxa gradients corresponded to physicochemical differences between sites.

The most powerful influence upon community structure in these springs was the affect of macrophytes, bryophytes and filamentous algae. High percentage of plant

cover corresponded with an increase in dipteran abundance and decreases in the abundances of mayflies, caddis and beetles. Other studies have also shown that invertebrate communities inhabiting macrophytes in New Zealand are dominated by Chironomidae, Mollusca, Crustacea and Trichoptera (Michaelis 1974, Death 2000, Hudson and Harding 2004). The results of my study are consistent with these findings, whereby sites with high levels of macrophyte cover were all numerically dominated by orthoclad and diamesine Chironomidae. Collier (1998) reported a lower percentage of mayflies, stoneflies and caddisflies on macrophytes than on wood in lowland Waikato streams. This was possibly due to lower dissolved oxygen concentration and water velocity levels in the macrophyte beds. During the day when plants photosynthesise they produce oxygen. However, at night they respire and consume oxygen which may reduce concentrations to a sub-optimal or lethal level for certain stream invertebrates (Kaenel et al. 2000). The possible effects of dissolved oxygen depletion on invertebrate communities, due to high macrophyte densities, cannot be assessed here as I did not sample dissolved oxygen levels nocturnally.

When present at low to medium percentage cover, macrophytes can increase the diversity of flow velocities by increasing velocity around weed patches and reducing velocity within them (O'Hare and Murphy 1999, Champion and Tanner 2000). However, at the high densities of macrophytes recorded in Collier's (1998) 18 lowland streams and in some of the springs in this study it is possible that flow diversity was sufficiently reduced to preclude high abundances of mayflies, stoneflies and beetles in favour of taxa preferring lower flow velocities.

Macrophytes and bryophytes also influence levels of food resources through detritus trapping and by providing a substrate for the growth of epiphytic algae (Suren 1992, Taniguchi et al. 2003). Due to the high structural complexity and levels of food resources, high abundances of some taxa would be expected, as reported by Collier (1999) in some lowland New Zealand streams. The mayflies, particularly *Deleatidium* spp, and the caddis *Pycnocentrodes* spp. and *Pycnocentria evecta* were the most abundant Ephemeroptera and Trichoptera taxa in this study. These taxa are primarily stone surface grazers and may not be able to negotiate the complex architecture of dense aquatic plants (Winterbourn 2000). The lack of periphyton on the light limited substrates beneath macrophyte beds and the entrapment of organic matter in the macrophyte, bryophyte and algal beds confer an advantage to taxa more able to negotiate and use aquatic plants as habitat. Dense macrophyte, bryophyte and algal growths are typically found in streams with stable flow regimes and low water velocities (Riis and Biggs 2001). The low levels of disturbance observed in my study may combine with low dissolved oxygen levels, low flow diversity and lack of suitable feeding substrate to make weedy springs more suitable habitat for Diptera, particularly Chironomidae, as opposed to Ephemeroptera, Trichoptera and Coleoptera.

My findings suggested that temperature was an important factor determining spring community composition. Mean temperature showed a positive relationship to axis 1 of the spring-source ordination, implying an increase in mayflies, caddisflies and beetles concurrent with a rise in average temperature. The opposite pattern was seen for dipterans, especially chironomids. My spring-source sites had a mean temperature of 6.5^{o}C to 10.5^{o}C. Huryn (1996) showed that instantaneous growth rates of

Deleatidium were maximal at a mean daily temperature of approximately 10°C. However the range of growth rates displayed in waters as cool as 5.5°C showed considerable overlap. Norrie (1969) found that flight activity of Trichoptera required a threshold temperature of 9.5-11°C. Boothroyd (1999) also found temperature to be a critical factor whereby Chironomidae in a Waikato stream exhibited more rapid growth rates during the warmer, summer months. Although some chironomids are known for their tolerance to environmental extremes, occurring in both geothermal and glacial habitats (Winterbourn 1969, Taylor 2001), the patterns observed from this study in chironomid abundance do not fit with our understanding of their reaction to temperature i.e. greater growth rate and potential abundance in warmer temperatures. This suggests that the relative shift in invertebrate communities seen across spring-source sites in this study may not be entirely due to the effects of temperature on growth and life-cycles. Minshall (1968), and Ward and Dufford (1979) both proposed that thermal constancy was an important factor at spring-sources. Although the results of my study suggest that temperature influences invertebrate communities, thermal constancy was not a consistent feature of these braided river springs. New Zealand's invertebrate fauna has been described as including numerous generalist taxa (Winterbourn et al. 1981), characterised by life history flexibility and a lack of ecological specialisation (Thompson and Townsend 2000). In particular, the asynchrony of life cycles seen in many taxa might explain why although temperature may affect growth rates and activity levels it does not appear to regulate life cycles in the same way as seen in the Northern Hemisphere. Thermally sensitive invertebrate species in the Northern Hemisphere may experience deleterious effects under constant temperatures whereas, members of the New Zealand fauna maybe less affected (Ward and Dufford 1979). Alternatively it is possible that the apparent effect of temperature

seen in my study actually represents another factor, or a combination of temperature and another factor, or factors.

My results also suggest that slope of a spring reach affects invertebrate communities. Increasing gradients were characterised by diptera, whereas low gradient springs had proportionally more mayflies, caddisflies and beetles. Slope values ranged between 0.07 and 1.54 degrees. This result is counter intuitive, as greater slopes would be expected to experience greater flow velocity and substrate disturbance, lower densities of macrophytes, and a shift in communities towards stony substrate taxa such as mayflies and caddisflies. In fact, the opposite pattern was seen here suggesting a spurious link between slope and invertebrate community composition.

Flow mediated disturbance has been shown to influence stream invertebrate communities in several studies (Resh et al. 1988, Death 1991, Lake 2000). The abundance of mayflies in this study, increased with increasing disturbance, temperature and discharge range (Figure 4). *Deleatidium* larvae reach their highest abundances in stony streams and are well adapted to life in highly disturbed habitats (Sagar 1986, Scrimgeour 1987, Quinn and Hickey 1990b). Their streamlined, dorso-ventrally flattened form allows them to resist high flow rates and their preference for grazing diatom rather than thick periphyton or filamentous algae (Winterbourn pers.comm.) also suits them for life in disturbed streams. I found that mayflies became more abundant as the size of the spring brooks decreased and suggests that smaller springs may have been less stable in terms of flow, than larger ones.

Spring-source invertebrate communities reacted predictably to the physical gradients measured. Disturbance/stability and the presence of macrophytes, bryophytes and filamentous algae determined the structure of invertebrate communities within these habitats. Although relationships between fauna and temperature were observed, it is suspected that the effect of mean temperature actually represents another factor and that fluctuations in temperature merely mirror the levels of disturbance.

4.4.2 Longitudinal changes in community composition

In Northern Hemisphere springs, a consistent pattern of increasing species diversity downstream from the source has been reported (Minshall 1968, Ward and Dufford 1979, Barquin and Death 2004). However, in New Zealand the opposite pattern of high diversity at stable sites, including springs, has been observed (Death and Winterbourn 1995). A recent examination of longitudinal diversity patterns in seven New Zealand springs indicated that diversity and abundance of benthic invertebrates tended to increase downstream from the source, although the pattern was not consistent for all springs (Barquin and Death *in press*). This result contrasts with my findings that taxa richness decreased with distance from the source.

New Zealand's invertebrate fauna has been described as one dominated by physical conditions, with biological interactions taking a secondary role (Thompson and Townsend 2000). As I found that disturbance and discharge range increased downstream an opportunity was presented to test models that predict diversity along disturbance gradients. Depauperate faunas in stable habitats have been attributed in part to an increase in predation on rare taxa induced by flow constancy or high habitat stability (Townsend et al. 1997). This is the basis for the low levels of diversity at

very stable sites predicted by the Intermediate Disturbance Hypothesis (IDH) (Connell 1978). In New Zealand, the generalist nature of many taxa and lack of life cycle synchrony may prevent strong competitive interactions that might result in exclusion of taxa from very stable sites. Furthermore, the high habitat complexity found at spring-source sites, due to the high coverage of macrophytes, bryophytes, and filamentous algae are likely to provide a greater diversity of niche and food resources capable of supporting higher invertebrate diversity.

Barquin (2004) compared invertebrate communities between springs in the Northern and Southern hemisphere (Spain and New Zealand) and found that predator populations in the Northern hemisphere sites were dominated by amphipods. In New Zealand, predators were far more diverse, but did not reach such high densities. Predators were also more diverse and relatively more abundant in springs than in run-off streams examined by Barquin (2004) in New Zealand. Similarly in my study predator richness and relative abundance declined with distance from the spring-source, along with the consequent fall in overall stability. Predatory taxa were diverse and consisted of Trichoptera (9 taxa), Diptera (3), Turbellaria (2), Coleoptera (2), Plecoptera (1), and Acari (1). Barquin (2004) hypothesised that a relatively high diversity of predators would maintain overall community diversity, as predators would regulate each other's densities. The downstream decline in diversity and relative abundance of predators observed in my study may contribute to the negative linear relationships between distance and overall diversity.

Concomitant with the decrease in predators away from spring-sources was an increase in the diversity and abundance of filter feeders. At the spring-source the only filter

feeders were *Austrosimulium* and ostracods however, within spring brooks the caddisflies, *Hydrobiosella* sp. and *Aoteapsyche colonica*, the mayfly *Coloburiscus humeralis*, a sphaerid bivalve, and larvae of a mosquito, *Culex* sp., were prominent. A likely explanation for the paucity of filter feeders at the spring-source is the lack of suspended organic matter in up-welling spring water, whereas suspended organic matter in spring brooks comes from allochthonous and autochthonous sources, and in both cases levels should increase with distance downstream. Thorup (1974) recorded a two-fold increase in detritus over a 50 m reach of a Danish spring brook. Thus, an increase in the taxa that specialise in feeding on suspended organic matter would be expected with increasing distance from the source.

4.4.3 Site age, dispersal and colonisation

In the Northern Hemisphere a distinct pattern has been reported, whereby insect dominance increases with decreasing time since glaciation (Hoffsten and Malmqvist 2000, Barquin and Death 2004). Thus more northerly springs, that were most recently glaciated, are inhabited principally by rapidly colonising insect taxa with greater powers of dispersal. My findings indicate that comparable colonisation dynamics can be observed within stable spring habitats on braided river flood plains over much shorter periods of time.

The Waimakariri basin has been extensively glaciated in the last 20,000 years, ceasing approximately 14,000 years ago (Gage 1977) and the spring fauna is insect dominated. However, aquatic habitats on the flood plain surface probably have a maximum age of 250 years, before being reworked by the main channel (Reinfelds and Nanson 1993). The presence of a certain taxon within a habitat is partly a

function of its powers of dispersal and its resilience/resistance to disturbance. At very stable, older sites we would expect to find the greatest number of taxa, and also those taxa with low powers of dispersal and low resilience/resistance to disturbance.

Most of the non-insect taxa found in this study are assumed to have low dispersal powers due to the lack of a terrestrial phase in their lifecycles (Malmquist 1991, Milner et al. 2000). For example, the molluscs *Potamopyrgus antipodarum, Lymnaea tomentosa* and sphaerid bivalves, generally disperse through water. Although capable of surviving high flows they would not normally be encountered in the disturbed main channel that links spring sites (Winterbourn 1983, Holomuzki and Biggs 2000). Additionally, the amphipods *Phreatogammarus fragilis* and *Paraleptamphopus* sp. are phreatic taxa, and probably disperse via groundwater pathways. Two flatworm species were found, neither of which would be expected to survive amongst the unstable substrate in the main channel environments that link spring up-wellings. *Prorhynchus putealis* (see title page) is phreatic and like other phreatic species may disperse via groundwater, whereas *Nepia montana* is common in hill slope streams, and may disperse throughout the braided river corridor via these peripheral habitats.

Although the alpine springs I studied may not become taxonomically dominated by non-insect taxa, we might expect some switch in community composition over time (Figure 8). In New Zealand, many lowland springs are dominated by non-insects (Death et al. 2004) and in sub-alpine regions older sites show a shift towards non-insect dominance. This suggests that rather than altitude and temperature restricting the local pool of invertebrates to predominantly insect taxa, it is the time taken by non-insect taxa to colonise each suitable site that structures spring communities.

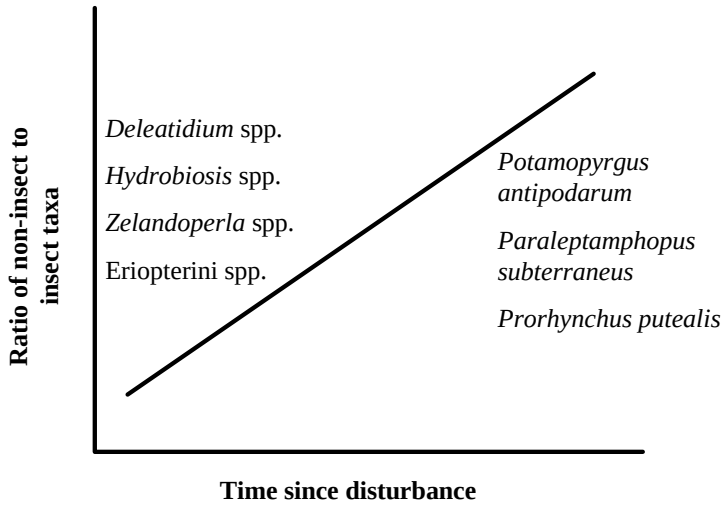

Figure 8. Conceptual diagram of the shift in community dominance from insect towards non-insect dominance with increasing time since disturbance. Taxa to the left of the graph have high powers of dispersal whilst those at the right are less effective at dispersal.

4.5 Conclusion

I found that older springs were more non-insect dominated than younger ones. This is thought to be the result of the slower rates of dispersal by non-insect taxa that lack a terrestrial life-cycle phase. This finding concurs with overseas studies which have suggested that post glaciation springs are insect-dominated but, that over time non-insect taxa colonise and begin to dominate communities.

Taxa diversity declined away from spring-sources. Higher diversity at spring-source sites is thought to be the result of higher habitat heterogeneity and the absence of competitive exclusion due to the generalist nature of New Zealand fauna. The high diversity of predators at spring sources may regulate predator density and increase

overall taxonomic richness. Spring-source habitats contained fewer filter feeders, than spring brooks and this is hypothesised to be due to low levels of suspended organic matter in up-welling spring water.

Spring-source invertebrate communities appear to be driven by the presence of macrophytes, bryophytes, algae, and stability. Aquatic plants influence dissolved oxygen levels, flow velocity, and food resources. They also represent a physical substrate with complex architecture, in stark contrast to gravel and cobbles. The patterns of increasing Diptera and decreasing Ephemeroptera with increasing plant cover conform to our understanding of the habitat preferences of these groups of insect taxa. The importance of macrophytes is investigated further with a small-scale manipulation described in the next chapter.

5

The effect of macrophytes on spring communities

Photo: Michelle Greenwood

5.1 Introduction

As Minshall (1984) states " the substratum is the stage upon which the drama of aquatic insect ecology is acted out". Most lotic invertebrates are predominantly benthic and therefore, the size, stability and characteristics of benthic substrates might be expected to have an over-riding effect on invertebrate community composition. Substrate provides living space, refuge from flow and predation, food resources and surfaces upon which food accumulates (Giller and Malmqvist 1998).

Considerable international literature exists on the relationships between substrate and benthic communities, and many workers have shown that aquatic plants provide rich habitat for a range of benthic taxa (Hynes 1970, Giller and Malmqvist 1998). A review of invertebrate-substratum relationships in New Zealand by Death (2000) confirmed that the composition of benthic communities differed between broad substrate categories, i.e., that macrophytes, moss, cobbles and gravel had different communities. Collier et al. (1999) showed that although taxonomic richness was low among macrophyte beds, invertebrate abundance may be high, and correlated with plant biomass. This finding is supported by other studies which have shown that high macrophyte biomass frequently supports communities dominated by one or two taxa such as the molluscs, *Potamopyrgus antipodarum* and *Physa acuta*, chironomids or crustaceans (Marshall 1973, Biggs and Malthus 1982, Death 1991, 2000).

The primary drivers of aquatic plant growth in New Zealand streams are light, substrate stability and flow regime (Biggs 1996, Reeves et al. 2004). Therefore, the relatively constant flow, and to a lesser degree constant temperature of springs, mean they are often heavily overgrown with macrophytes and bryophytes (Death et al.

2004). Shaded sites tend to be dominated by bryophytes, although bryophytes are by no means absent from sites with no shading, where they coexist with angiosperm macrophytes (Suren 1993, Reeves et al. 2004). The effect of flow on aquatic plants is inextricably linked with substrate stability. All large aquatic plants require a stable substrate, however, macrophytes and bryophytes differ in their resistance to the shear stress of current. Bryophytes may be found in torrential mountain streams (Suren 1991) whereas macrophytes are rarely found in velocities above about 1m/s and biomass usually decreases as velocity increases (Riis and Biggs 2001, Reeves et al. 2004).

Given the global recognition that substrate exerts a major influence on benthic communities, and that fauna differ in terms of taxonomic composition, richness and abundance between aquatic plants and stony substrates, it is not surprising that my findings presented in chapter 4 support the view that benthic invertebrates of springs are greatly influenced by the presence of aquatic plants. However, researchers in New Zealand and elsewhere have suggested that spring communities are driven by a range of factors, which vary in temporal and spatial scale. The effects of historical glaciation, altitude and distance from the sea have been suggested as playing important roles in structuring spring invertebrate communities (Vannote et al. 1980, Williams 1991, Hoffsten and Malmqvist 2000, Barquin 2004). Water chemistry (specifically hardness) (Glazier 1991), temperature constancy (Minshall 1968, Ward and Dufford 1979), flow velocity and disturbance (Minshall 1968, Glazier 1991, Barquin and Death *in press*) have been shown to effect invertebrate communities, as do biological interactions, such as competition and predation (Cushing 1996, Barquin 2004). Although Barquin (2004) and Death (1991) described associations between

substrate, macrophytes, and spring invertebrate communities in New Zealand, no specific tests of the influence of aquatic plant presence/absence on spring fauna have been made.

The aim of the work reported in this chapter was to experimentally investigate the effect of aquatic plant removal upon spring invertebrate communities.

5.2 Methods

5.2.1 Site selection

Four short reaches below spring-sources were selected. All four springs emerged from the base of a flood plain terrace upstream of the confluence of the Hawdon and Waimakariri rivers and were within 50 m of each other. The four springs, which were between 7 and 10 m long, drained into a small spring brook bordering One Tree Swamp (Figure 1 & 2) which eventually joins the main channel of the Waimakariri River. All four sites had similar channel morphology, being broad areas of diffuse up-welling with a low gradient, abundant macrophytes and bryophytes, and similar cobble dominated substrate (Figure 1). The dominant macrophyte was *Callitriche stagnalis* (water starwort), which covered most of the area of the spring-sources. Various unidentified bryophytes were also present

5.2.2 Experimental design

Between 5th January and 9th February 2005 a macrophyte manipulation experiment was conducted. On 5th January, within each spring-source, eight 1m^2 quadrats were selected (Figure 3). Half of these quadrats, selected at random, were cleared of all macrophyte and bryophyte material, whilst aquatic plant material in the others was

left untouched, as controls. Some bryophytes were difficult to remove from the larger substrates, so the substrates were removed. To avoid a substrate size effect on benthic communities, aquatic plant-free substrates of equivalent size taken from within the springs, were placed within the quadrats. In all quadrats benthic invertebrate densities, macrophyte biomass and inorganic benthic substrate chlorophyll-*a* were measured on the 9th February 2005. Stage height and water temperature was recorded every 30 minutes for the duration of the experiment in each spring using four TruTrack WT-HR 1000 water height and dual temperature data loggers.

Figure 1. Manipulation sites viewed looking west along the flood plain terrace.

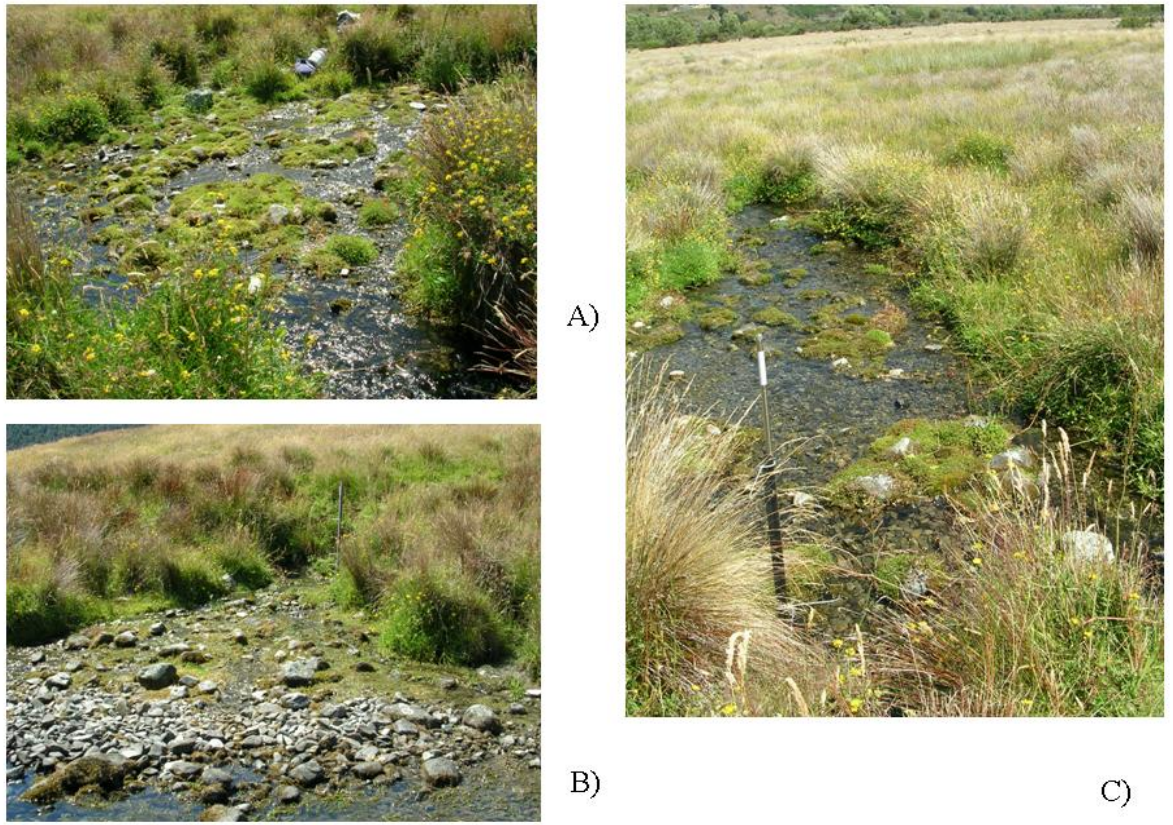

Figure 2. Spring 1 (A), spring 4 (B), and spring 2 (C) at the base of a flood plain terrace adjacent to One Tree Swamp. (Chapter 3, Figure 1)

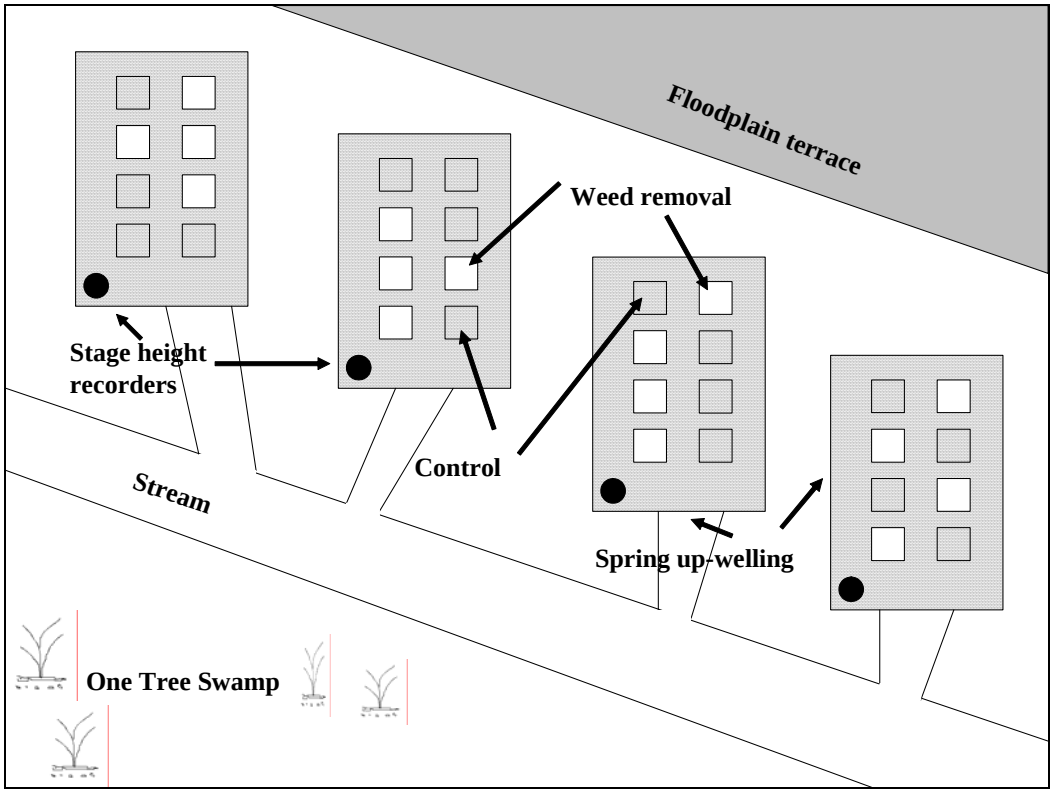

Figure 3. Schematic diagram of the macrophyte manipulation experiment. Quadrats in springs were placed randomly and spring-sources drained into the associated spring brook.

5.3.3 Invertebrate and weed sampling

After 30 days a Surber sampler (0.6 m^2, mesh size 250 µm) was placed randomly within each 1 m^2 quadrat to collect benthic invertebrates. In control quadrats (macrophytes present) all macrophytes and bryophytes within the Surber sampler frame were placed in a bucket and washed thoroughly to remove all invertebrates. Aquatic plant biomass was returned to the laboratory, oven dried (at 45^o) and weighed (to 0.01g). Invertebrate samples were preserved in 70% ethanol in the field and sorted in the laboratory under 40x magnification. Identifications were made from keys by Winterbourn (1973), Chapman and Lewis (1976), Cowley (1978), McLellan (1998), Winterbourn et al. (2000), and Smith (2001). Identification was carried out to the

lowest taxonomic level possible, except for Oligochaeta which were not differentiated below order and Chironomidae which were not separated below tribe.

5.2.4 Periphyton sampling

At the end of the experiment periphyton biomass on stones, within control and treatment quadrats, was estimated by measuring chlorophyll-*a*. Three stones devoid of macrophytes or bryophytes were randomly collected from each quadrat, within each treatment, and were placed in 100 ml of 90% ethanol for 24 hours at 4^{o}C in the dark. The concentration of extracted chlorophyll-*a* was measured using standard spectrophotometric methods (HACH 1990) and the following formula:

$$chla(mg/cm^2) = \frac{12\ x\ (665-750)\ x\ 100}{area\ x\ path\ length}$$

Where path length is 2.6

The surface area of each pebble was calculated by tracing the outline of stones, weighing the area of paper, then using the following formula:

Surface area (cm^2) = (Weight of stone area on paper / weight of 1cm^2 of paper)

Periphyton was expressed as µg Chlorophyll-*a* / cm^2.

5.2.5 Data treatment and statistical analysis

Rarified taxonomic richness and Shannon's index of evenness were calculated as outlined in chapter 4, using PRIMER (Clarke and Warwick 1994). Rarefaction was standardised to the lowest number of individuals in any one sample (348). Rarefied

diversity values are preferable to taxonomic richness for comparing habitats when either sample sizes differ or habitats contain different densities of individuals. Rarefaction calculates the number of species that would be expected from samples of a standard size or based on a particular abundance (Magurran 1988). As densities were very different between treatments it was decided that rarefied values would provide a more appropriate comparison of true taxonomic richness between treatments.

The ANOVA model used for community analysis was a mixed effects model with treatment as a fixed effect, and springs as a random effect. Multiple comparisons were controlled for by the use of MANOVA, with univariate ANOVAs conducted on each response variable. Tukeys post hoc test was used to look for differences between treatments. The same ANOVA model was used to compare chlorophyll-*a* levels between treatments, and a Kruskal-Wallis test was used to compare weed weight between control treatments as data could not be normalised. Analyses were performed in Systat v.10 (2000)

5.3 Results

5.3.1 Physical habitat: flow and temperature

Temperature and stage height in all four springs were very similar over the entire 30 day experimental period (Figure 4). Water temperature fluctuated no more then 4.4^{o}C and stage height by no more than 30 mm in any spring.

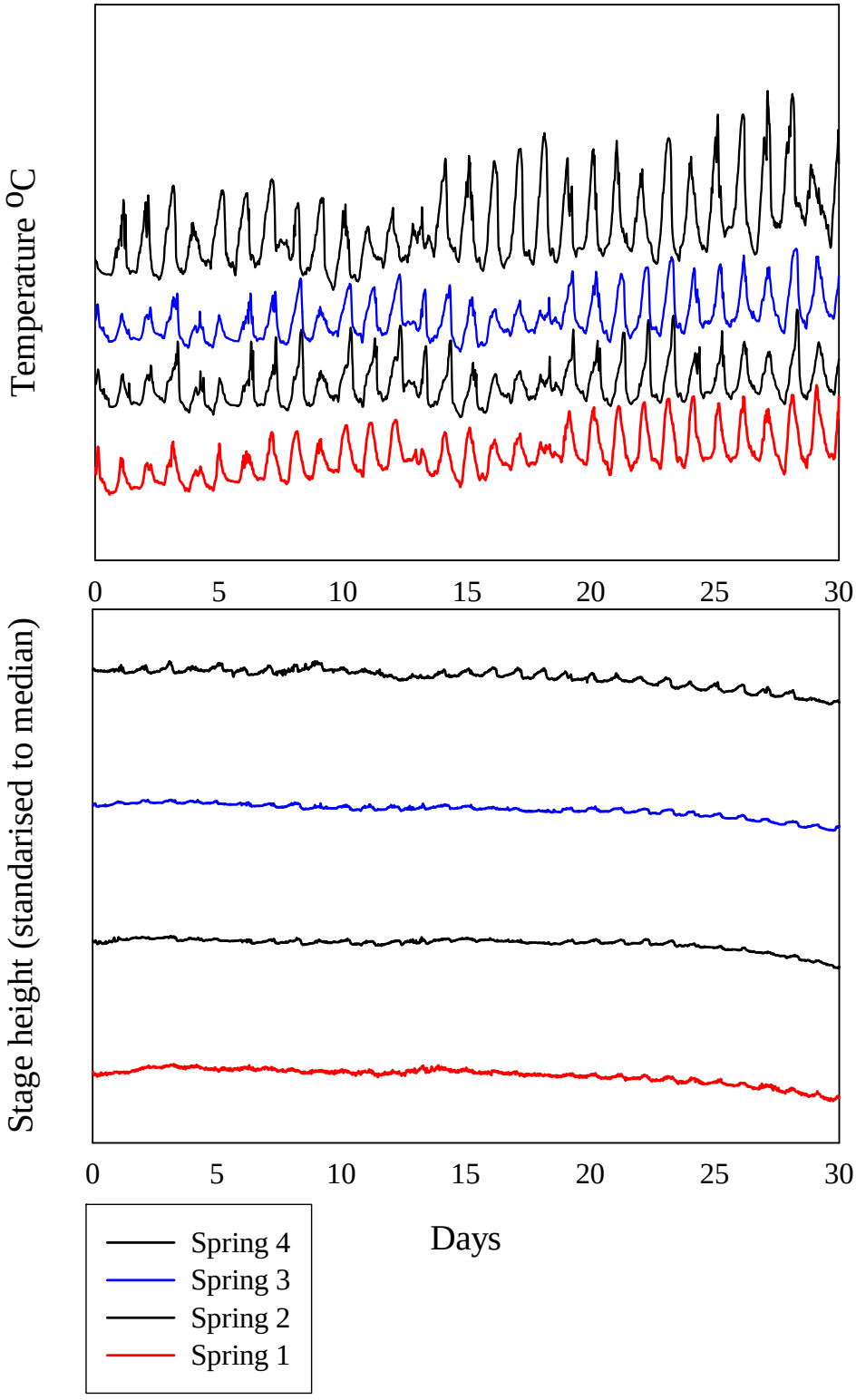

Figure 4. Water temperature and standardised stage height within the four springs over the 30 days of the experiment.

5.3.2 Periphyton and macrophytes

After 30 days periphyton levels were significantly higher in quadrats from which aquatic plants had been removed (Treatment effect, $F=42.55_{1, 86,}$ $p=0.007$) (Figure 5). Some variation was found between springs (Spring, $F_{3, 86}$, $p=0.003$) which was attributed to site disturbance by cattle prior to the manipulation, however there was no treatment x spring interaction effect (Interaction, $F=0.382$, $_{3, 86,}$ $p=0.766$) suggesting that treatment effects were consistent across springs.

Aquatic plant biomass in the control quadrats ranged from 11.7g – 38.5g and did not differ significantly between springs (Kruskal-Wallis $W=0.944$, $p= 0.815$). Removal quadrats remained devoid of non-algal aquatic plant biomass.

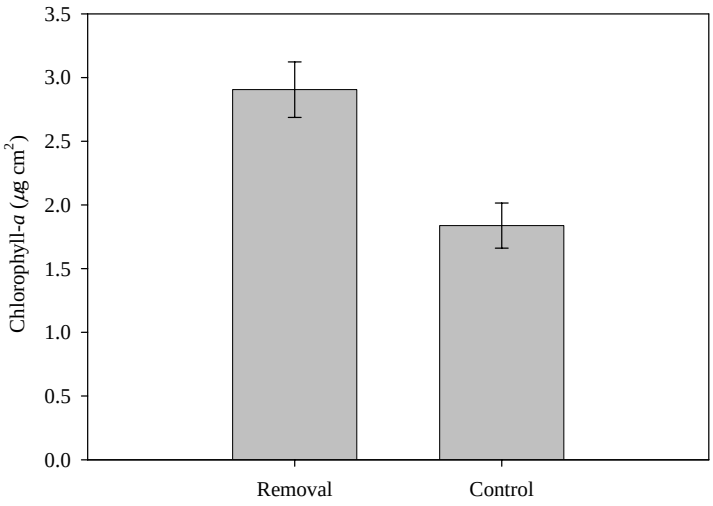

Figure 5. Mean chlorophyll-*a* levels (µg cm^2) on stones taken from removal and control (macrophytes present) quadrats. (± 1 SE, calculated from all stones in all quadrats combined).

5.3.3 Benthic invertebrates

Overall, spring communities contained 12 dipteran taxa, eight caddisfly taxa, one mayfly, *(Deleatidium*), and two stonefly taxa, *Austroperla cyrene* and *Zelandobius*

pilosus. The common snail, *Potamopyrgus antipodarum* was the only mollusc collected in these springs. The flatworms were represented by the triclad, *Neppia montana*. and the allocoel *Prorhynchus putealis*, a phreatic flatworm which has previously been found in springs and trout redds in the beds of up-welling reaches of Canterbury and Southland spring-fed rivers, as well as springs in the Cass basin (Percival 1945). Also present, were the aquifer-dwelling amphipods *Paraleptamphopus* sp. and *Phreatogammarus fragilis*, both of which are known from springs, up-welling river reaches and groundwater samples (Chapman and Lewis 1976). On average springs were numerically dominated by *Potamopyrgus antipodarum*, orthoclad chironomids, *Pycnocentrodes*, diamesinae chironomids and the mayfly *Deleatidium*. However, the relative abundances of taxa were altered by the removal of macrophytes.

Taxonomic richness was greater in the control quadrats than the removal quadrats, but was the same among springs (Table 1, Figure 6a). However, rarefied taxonomic richness indicated no difference between treatments (Figure 6b).

Table 1. Mixed model MANOVA and ANOVA results comparing invertebrate communities, with spring as a random factor and treatment a fixed factor. Results in bold are significant at *p*= 0.05. C = control, R = removal.

Multivariate results

	D.f.	Wilk's lambda	F	*p*
Springs	24, 47	0.045	39.437	< 0.001
Treatment	24, 47	0.045	3.736	< 0.001
Springs * Treatments	24, 47	0.199	1.459	0.132

Uni-variate results

Variable	Treatment (d.f. 1, 3)	tukey	Spring (d.f 3, 23)	Interaction (d.f. 3, 23)
Species richness	F=15.140, *p*= **0.030**	C>R	F=2.375, *p*= 0.960	F=0.338, *p*= 0.798
Rarefied taxa diversity	F=8.4800, *p*= 0.061	C=R	F=3.720, *p*= **0.026**	F=0.085, *p*= 0.968
Shannon's evenness	F=82.660, *p*= **0.002**	C<R	F=0.483, *p*= 0.698	F=1.318, *p*= 0.293
Abundance	F=136.70, *p*= **0.001**	C>R	F=5.902, *p*= **0.004**	F=0.368, *p*= 0.776
% Mayflies	F=505.90, *p*< **0.001**	C<R	F=3.712, *p*= **0.026**	F=0.343, *p*= 0.794
% Caddis flies	F=98.400, *p*= **0.002**	C<R	F=5.925, *p*= **0.004**	F=1.200, *p*= 0.332
% Diptera	F=1.3830, *p*= 0.320	C=R	F=4.134, *p*= **0.018**	F=6.130, *p*= **0.003**
% *Potamopyrgus*	F=4.7580, *p*= 0.117	C=R	F=5.681, *p*= **0.005**	F=5.741, *p*= **0.004**

Significantly more individuals were found in the control treatments than in the removal quadrats (Figure 6c). Concomitant with a highly significant increase in abundance, a fall in evenness was observed in the control treatments compared to the removal treatments (Figure 6d).

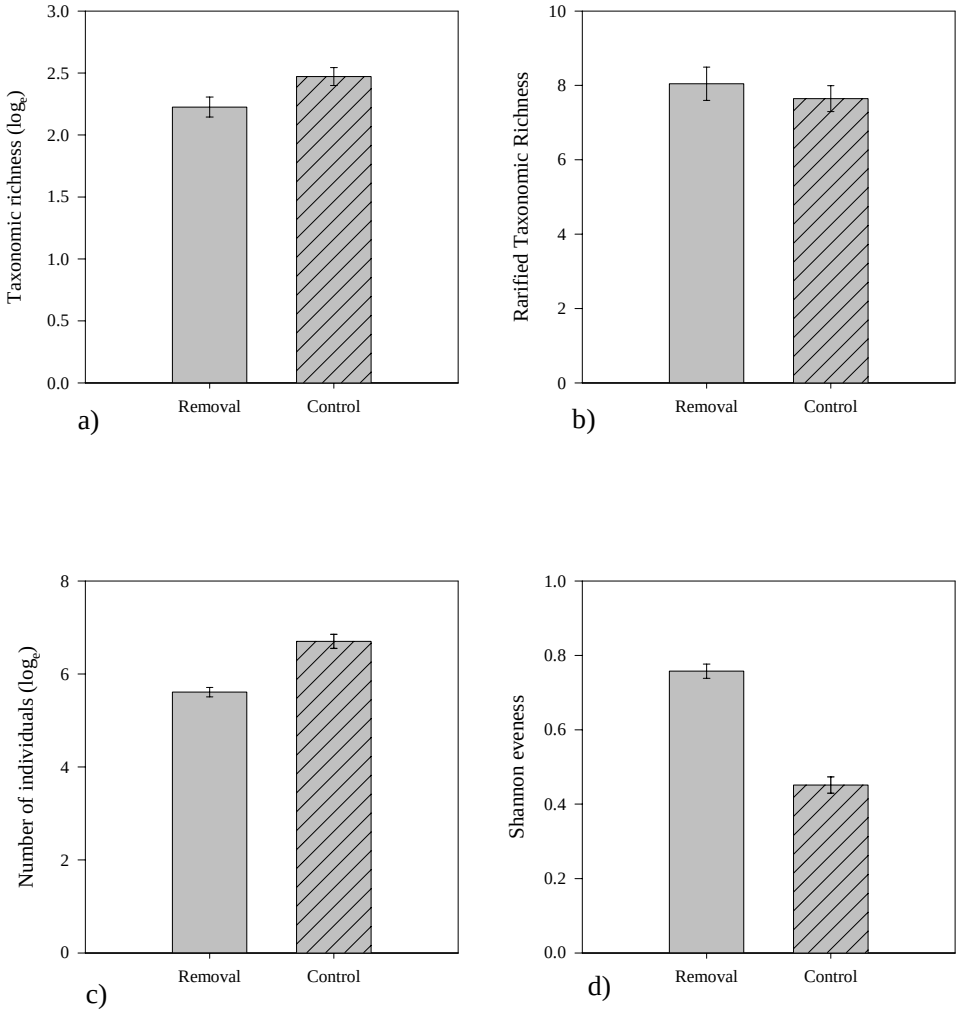

Figure 6. Comparison of invertebrate community indices in removal and control treatments. (mean ± 1SE calculated from all quadrats combined).

The relative abundance of mayflies was much higher in the removal quadrats than the control (Figure 7a,). Similarly the relative abundance of caddisflies was higher in the removal treatment (Figure 7b).

Mayflies and caddisflies were replaced by dipterans, which showed a significant proportional decrease within the cleared treatment (Figure 7c). ANOVA indicated no treatment effect for diptera (Table 1), but a significant interaction effect. This was due to one spring in which dipterans were proportionally more abundant in the removal treatment. However, the overall trend of strong diptera dominance in controls is clear.

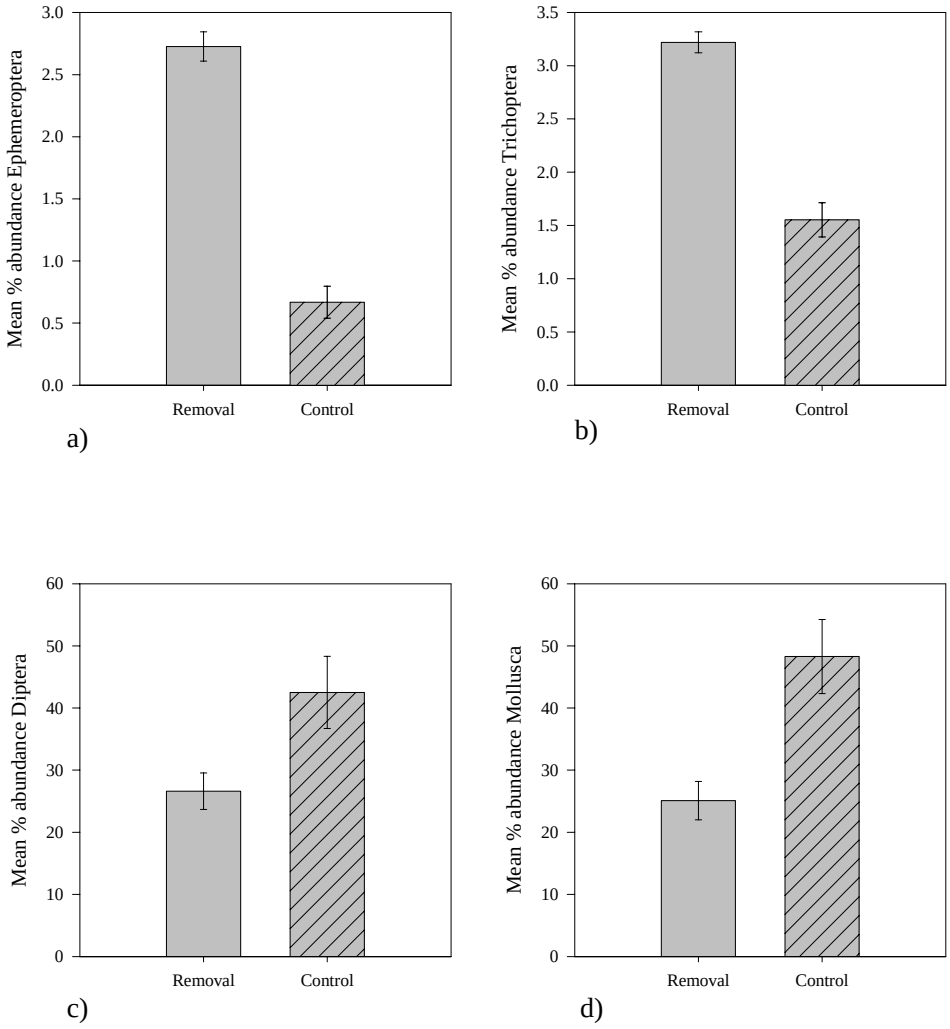

Figure 7. Mean % abundance of Ephemeroptera, Trichoptera, Diptera and Mollusca in removal and control treatments (mean ± 1 SE).

The mean abundance of molluscs, which were entirely *Potamopyrgus*, was greater in the control treatments than the removal treatment (Figure 7d). No significant treatment effect was found due to high variability between springs, however, the significant interaction term and inspection of an interaction plot indicate that a treatment effect does occur and the pattern was consistent across springs.

In summary, although there was some variation between and within springs, macrophyte removal resulted in a proportional shift in community dominance from Diptera and Mollusca in the control towards Ephemeroptera and Trichoptera in the removal. Overall, abundance was lower in the removal, evenness increased, but species richness remained relatively constant.

5.4 Discussion

5.4.1 Taxonomic richness

Raw taxa numbers indicated that aquatic plants in spring-source habitats supported a higher taxonomic richness than stony substrates. This finding is in accordance with results of several overseas studies suggesting that aquatic plant invertebrate communities are highly diverse (Hynes 1970, Giller and Malmqvist 1998). Furthermore, several other New Zealand studies have recorded greater diversity at stable sites (often defined by the presence of aquatic plants), than at those which have experienced some form of disturbance (Death 1991, Barquin 2004). However, after rarefaction the difference between taxa numbers within the two substrates was no longer significant. It is possible that because aquatic plants support much higher densities of benthic invertebrates that taxonomic richness is higher by chance alone. When we consider the spatial and temporal scale of this manipulation the result becomes less surprising. The macrophyte removal quadrats were 1 m^2 and embedded within a spring bed matrix of unaltered, and aquatic plant dominated, habitat. It is therefore reasonable to expect movement of individuals from within each treatment quadrat, and that taxa present in the spring might be relatively mobile across treatments. Furthermore, my manipulation was run for little over four weeks, which may not allow adequate time for colonisation of taxa from outside the immediate area

of the spring, with a preference for inorganic substrates in spring-source habitats. Thus, the diversity results of this manipulation need to be considered in the context of local habitat preferences of the taxa present, rather than the effect of macrophytes on colonisation and dispersal dynamics across the riverscape. Short term manipulations are more likely to effect changes in relative abundance and equitability within habitats, than the pool of taxa present.

5.4.2 Density

My results concur with findings in New Zealand and overseas, that macrophytes support higher abundances of benthic invertebrates than inorganic substrates (Giller and Malmqvist 1998, Death 2000). A number of mechanisms could explain this phenomenon.

First, macrophytes provide complex 3-dimensional living space to benthic invertebrates. Although cobble/gravel substrates do provide a third dimension of living space, the hyporheic zone (Stanford and Ward 1988, Jones and Holmes 1996, Jones and Mulholland 2000), this is often not sampled by conventional techniques, e.g., a Surber sampler. Macrophyte beds extend available habitat up into the water column and therefore, equate to a larger volume of habitat than is sampled by conventional techniques (O'Hare and Murphy 1999).

Secondly, macrophyte and bryophyte beds provide protection from de-faunating flow velocities (Suren 1991, Humphries 1996, O'Hare and Murphy 1999). This allows the density of invertebrates able to live on aquatic plants to reach high levels.

Furthermore, aquatic plant communities have been shown to be depauperate in predatory taxa (Tokeshi 1994 in Giller and Malmqvist). The main predators in my study were four free-living caddis larvae, two flatworms, a chironomid and a ceratopogonid. Whilst *Prorhynchus putealis*, Tanypodinae and ceratopogonids occurred at low densities in all treatments, the predatory caddis were found in higher numbers within the aquatic plants than on the cleared substrata, whereas the flatworm *Neppia* preferred the inorganic substrate. Overall, in the removal treatment 1.9% of individuals were predators compared to 0.77% in the control treatment. The most abundant taxon in both treatments was *Potamopyrgus antipodarum* which probably has some protection from predation due to its calcareous shell and operculum.

Finally, the high abundance of benthic invertebrates within aquatic plant beds were probably supported by elevated levels of food resources. Living macrophytes and bryophytes rarely provide a direct source of food for New Zealand benthic invertebrates, but epilithon and detritus that collects on them are a constant source of food (Suren 1992, Death 2000). Sand-Jensen (1998) found that patches of *Callitriche cophocarpa* in lowland Danish streams increased entrainment of fine particles and enriched sediment under these stands with organic matter. This situation would be particularly suitable for the ubiquitous snail *Potamopyrgus antipodarum* which can switch between periphyton and detritus food sources (Dorgelo 1991 in Winterbourn 2000). After an extensive study of bryophyte-invertebrate associations near Arthur's Pass, close to my study area, Suren (1990) concluded that the higher levels of periphyton and fine particulate entrainment associated with mosses contributed to the differences observed between bryophyte and cobble invertebrate communities. Thus, it is likely that invertebrate abundance on aquatic plants was enhanced by the

increased living space they provide, benign flow conditions, relatively low levels of predation and high food resource availability.

5.4.3 Taxonomic equitability

The degree of equitability among taxa, or evenness, is sometimes used as a measure of anthropogenic impact upon streams (Harding et al. 2000, Quinn 2000, Suren 2000). Hardy species, that are resistant to change, become proportionally more dominant within the community, and impacted sites exhibit reduced evenness. However, variations in equitability have been described in un-modified systems, specifically within macrophyte beds (Death 2000). The results of my manipulation indicate that evenness among aquatic-plant dwelling invertebrates is low and communities become dominated numerically by a small number of taxa, consistent with the findings of other researchers (e.g., Collier 1990). Thus, significantly greater densities of *Potamopyrgus antipodarum* and chironomids were seen in macrophyte habitats than on cleared substrata.

5.4.4 Shifts in community composition

The shift in community dominance of quadrats from chironomids and molluscs in control quadrats to mayflies and caddis in removal quadrats is consistent with our understanding of the ecology of these taxa. *Deleatidium* and the cased caddisflies *Pycnocentrodes* and *Pycnocentria* are predominantly stone surface grazers (Winterbourn 2000), which ingest algal periphyton, and detritus that becomes entrained within the algae on stone surfaces. The lack of light below aquatic plant beds, significantly reduced levels of periphyton on stones, and therefore, the algal food resources of these mayflies and caddisflies. Conversely, the protection from

high flows and predation, plus the possibility of enhanced levels of epilithon and organic matter retention on the aquatic plants themselves, provide conditions more suitable for mollusc and chironomid taxa, that may be more capable of negotiating the complex architecture of plants.

5.5 Conclusions

Macrophytes have been show to have a strong influence on the structure of benthic invertebrate communities in New Zealand lowland streams, drains and rivers (Marshall and Winterbourn 1979, Biggs and Malthus 1982, Rooke 1984, 1986, Collier et al. 1998, Collier et al. 1999). However, the effect macrophytes have in structuring invertebrate communities within New Zealand spring-sources had not been investigated prior to my study. My manipulation compared spring-source communities between macrophyte and cobble substrates, and demonstrated the shifts in invertebrate community composition. The results highlight the importance of substrate, particularly aquatic plants, in structuring spring invertebrate communities in New Zealand.

6

Synopsis

6.1 The physical phenomenon

Springs were found to be abundant in braided river flood plains, which were located in the middle and lower reaches of the rivers considered in this study (Chapter 2). This is not to say however, that springs are unique to braided reaches in terms of the river corridor or landscape. So, why are springs such a regular feature of the flood plains of many New Zealand rivers?

A spring is defined as a natural outflow of groundwater, and exists at the point where the water table intersects with the surface of the ground. Thus, a pre-requisite for spring occurrence is a riverbed with a highly permeable substrate. Furthermore, pre-requisites for a stable spring are a consistent supply of water and a substrate that remains permeable. The highly disturbed flood plain of a braided river fulfils these criteria and results in the co-existence and interdependence of highly contrasting physical environments.

The braided rivers of the South island were formed in the last 20, 000 years as a result of glacial action, rainfall and snow melt (Gage 1977). Continuous erosion of friable bed rock, coupled with high and unpredictable rainfall characteristic of a maritime, mountainous country, positioned perpendicular to the predominant flow of weather systems, maintains these rivers in a constant state of morphological dynamism. The alluvium which has accumulated within expansive glacial valleys is highly permeable, and carries an alluvial aquifer within a sinuous lattice of preferential flow paths, which are an heterogeneous sediment matrix laid down by former migrations of the river channel (Huggenberger et al. 1994, Woessner 2000, Poole et al. 2002) (Chapter 1). During base flow conditions the aquifer loses water to the river, which may

constitute the majority of main channel flow at such times (Hynes 1983). During floods however, the river loses flow to bank infiltration, reducing flood level and recharging the aquifer (Brunke and Gonser 1997). Thus, whilst successive discharge and recharge of the aquifer has a buffering effect on the discharge regimes of rivers, the aquifer also provides stable inputs of water at spring up-welling points, despite the irregularity of precipitation in each catchment.

Over time, reductions in porosity and hydraulic conductivity may occur due to the intrusion of fine sediments into interstitial spaces. This clogging of the top layer of the channel sediments is termed colmation (Brunke 1999). Colmation is characterised by tightly packed, compact sediments with low porosity and permeability. However, under natural flow regimes colmation is removed by high flow events involving bed load movements (Brunke and Gonser 1997). Impoundment of the River Spol in Switzerland, resulted in decreased discharge and a regular flow regime lacking the competence to transport inorganic sediment (Murle et al. 2003). The effect of impoundment was to allow the gravel bed to become clogged however, experimental floods reduced embeddedness, and increased the heterogeneity of channel depths and types. A similar experiment conducted in the River Rhone flood plain revealed the importance of high flow events for maintaining connectivity between surface-waters and ground-waters (Claret et al. 1999). The pristine headwaters and natural flow regimes of many rivers are critical to maintenance of ground-water surface-water connectivity, as they provide the source of flow to many springs found along flood plain reaches (Poff et al. 1997).

Although in complete contrast to the highly disturbed, flood prone and unstable rivers of which they are a part, it is these flow regime and disturbance characteristics that allow braided river springs to form, and remain stable. Without high levels of disturbance in the main channel, hydrological connectivity would be reduced, and result in the loss of springs, which are "hotspots" of biodiversity within the braided river corridor (Chapter 3).

6.2 Dynamic stability

In the upper Waimakariri River, springs contain a large proportion of the rare invertebrate taxa within the river corridor (Chapter 3). Furthermore, I found that older springs had a higher percentage of non-insect taxa, which take longer to disperse. So, how do the taxa unique to springs initially colonise these habitats?

The Waimakariri River, into which both spring and hill slope streams flow, is highly disturbed and does not possess a continuous flood plain aquifer along its route to the sea. Many non-insect taxa, which disperse almost exclusively through water, are thought to have originated in marine environments (Hynes 1970) and migrated upstream. However, contemporary conditions between the study area and the mouth of the Waimakariri River are prohibitive to migration, either within the river or its aquifer. The initial colonisation of sub-alpine springs by non-insect taxa, after the glaciers had receded, may have occurred either during a period of relative climatic stability in the catchment, or incrementally via peripheral and microhabitats. Presumably either route could have supported discrete colonisation events into the braided river corridor, but colonisations might not be common. The numerous insect taxa found only within springs have greater powers of dispersal because most have a

terrestrial phase in the life cycle. However, these insects are only located in the small, discrete, and temporary (250 years) habitats represented by springs. So, the question becomes how have these populations, isolated in a “sea of disturbance”, persisted?

Habitat turnover in braided river corridors has been described as an example of a shifting mosaic steady state model, whereby despite high turnover the relative proportions of each habitat remain constant through time (Arscott et al. 2002, Hauer and Lorang 2004). If this is the case for the braided reaches of the Waimakariri River included in my study one can hypothesise that at the catchment scale spring invertebrate diversity could be maintained, in the absence of further colonisation from outside the area. Despite a habitat turnover rate for this stretch of river, estimated to be in the order of 250 years (Reinfelds and Nanson 1993), diversity could be maintained by local, short range dispersal between patches reminiscent of metapopulations (Begon et al. 1996). Figure 1 illustrates the relationship between local diversity within individual springs and river corridor diversity. The maintenance of locally isolated populations in springs within highly disturbed braided river systems would be possible through local dispersal, via temporary, unsuitable or groundwater habitats, as constant proportions of habitat are available despite high turnover. Biodiversity in springs, particularly of taxon with low powers of dispersal, is dependent upon the stability of proportional habitat diversity, which is a feature of the pristine environments found in some New Zealand braided river systems.

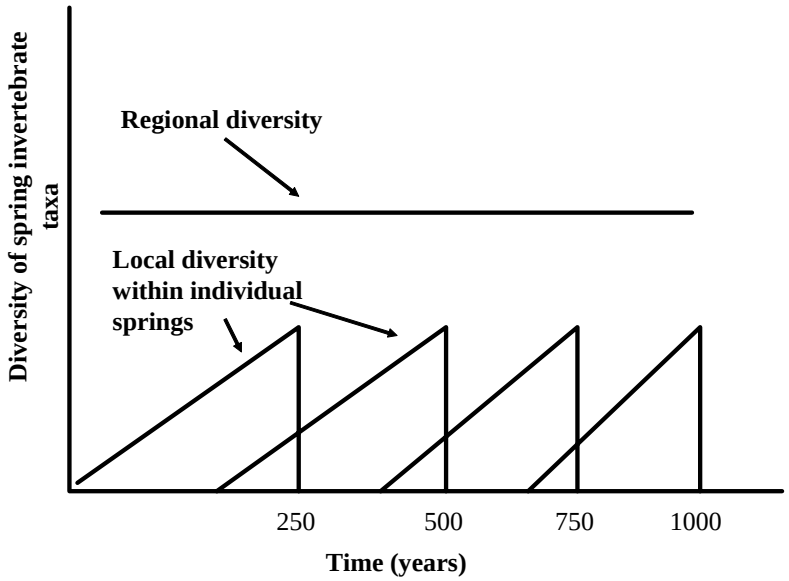

Figure 1. Conceptual diagram of the maintenance of regional diversity (species pool) in springs despite high habitat turnover and fluctuating local diversity.

6.3 Anthropogenic impacts

My South Island spring mapping survey revealed that 16% of all springs were associated with anthropogenic structures (Chapter 2). In my Waimakariri River field survey the Klondyke spring complex was located in an area of flood plain sheltered by two sets of flood retention works (Figure 2). The Klondyke springs contained a diverse invertebrate fauna (including phreatic taxa), which was similar to the communities in more naturally occurring springs (Chapter 3). Thus, the impact of anthropogenic structures upon corridor bio-diversity and habitat heterogeneity was a positive one. However, not surprisingly, it is also possible that human impacts in the alluvial corridor can be negative.

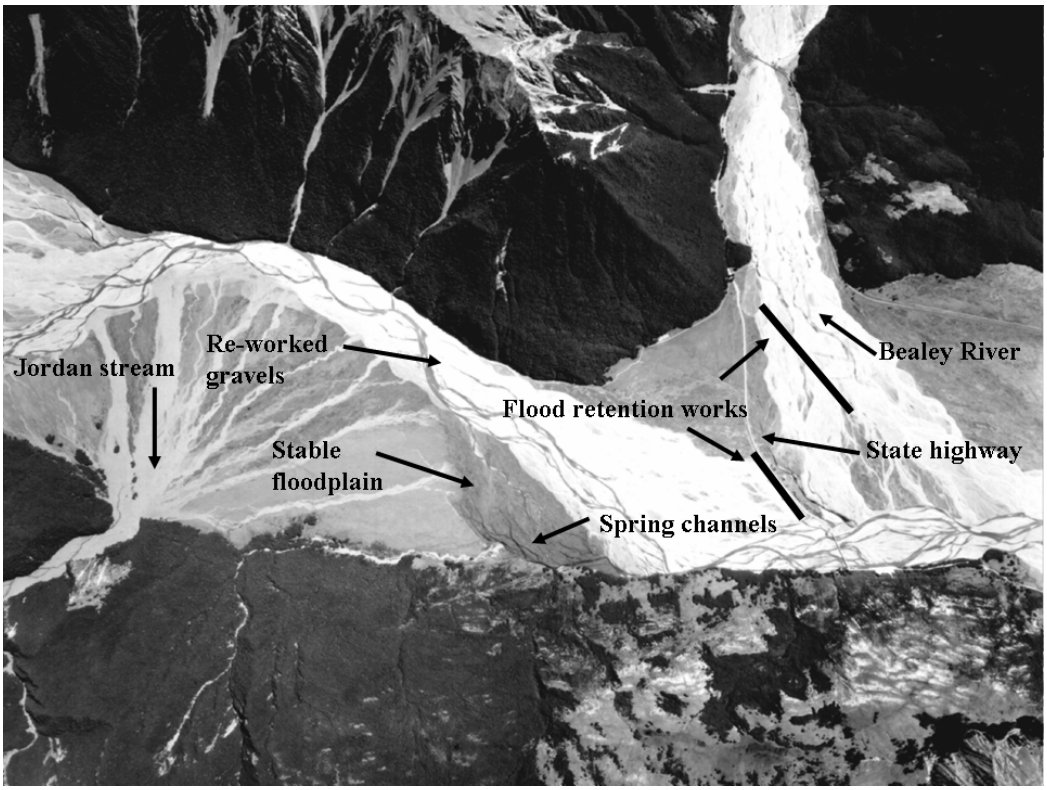

Figure 2. Waimakariri River at its confluence with the Bealey River. Flood retention works around the Klondyke spring up-welling location are labelled.

Channelisation of reaches in many large New Zealand rivers has been undertaken to create farmland and prevent river migration (Young et al. 2004). Constriction of the river channel can cause changes in local aggradation and degradation, which may impact upon interactions with the aquifer and thence water supply to springs. A 0.5 m drop in the bed of the lower Motueka River was predicted to reduce summer aquifer recharge by 24% (Basher 2003 in Young et al. 2004). Furthermore, disconnection of the river from its flood plain will alter successional dynamics within spring habitats. Following the construction of flood control barriers, already extant springs will remain undisturbed, and no new springs will be created by the reworking of alluvial gravels and river channel migration. Spring-fed habitats therefore will tend towards later successional stages. In the long term, construction of flood control barriers may

result in the reduction of invertebrate and habitat diversity seen in many channelised European rivers (Claret et al. 1999, Pringle 2001, Hohensinner et al. 2004).

In many parts of New Zealand, braided rivers are contained within flood retention works to protect farmland. This has resulted in numerous stable springs being formed in the lee of flood retention works. Unfortunately, modern, intensive farming techniques are often detrimental to stream health (Quinn 2000, Parkyn and Wilcock 2004). Whilst spring occurrence may be increased by anthropogenic activities, the benefits to biodiversity are offset by subsequent degradation of the habitats.

Impoundment is a feature of many large rivers, globally, and as already mentioned can alter physical conditions substantially below dams. Since 1950, 10,000 km^3 of water, (more than five times the volume of water in all the worlds rivers), has been impounded in reservoirs globally (Rosenberg et al. 2000). Despite the daming of many of New Zealand's largest rivers, the Clutha, Waitaki, Waikato, Rangitaiki and Waiau, little research has been undertaken on its geomorphological and ecological consequences for ground-water surface-water exchange, or spring complexes. However, there is a wealth of overseas and New Zealand literature upon the general downstream effects of flow regulation via impoundment (Henriques 1987, Rosenberg et al. 2000). Dams and river diversions have proven to be primary destroyers of aquatic habitat, contributing to the destruction of fisheries, extinction of species and the loss of ecosystem services vital to the human economy (Pringle et al. 2000, Rosenberg et al. 2000). In particular the negative impact of flow regulation upon the morphological and successional diversity of flood plains has been highlighted (Ward and Stanford 1995, Gilvear 2004, Hohensinner et al. 2004, Choi et al. 2005). A

reduction in channel forming flows and sediment load reduces the rate of channel migration, which is important for maintaining high levels of habitat diversity. High biodiversity in flood plain ecosystems is a function of the diversity of water bodies with differing degrees of connectivity with the main channel, and the range of successional stages present due to historic channel migrations. The effect of flow regulation is similar to that of channelisation, in that it truncates the fluvial system and disconnects the river from its flood plain (Hohensinner et al. 2004). The successional trajectories of flood plain elements trend towards maturity, which may involve changes to invertebrate communities due to competitive exclusion (Begon et al. 1996). In effect the dynamic equilibrium is broken and may take in excess of 100 years to re-establish (Gilvear 2004).

Since the 1930s the lower Waitaki River, South Island, has been drastically altered, predominantly by impoundment for hydroelectrical power generation. The reduction in flow variability and sediment input due to impoundment has caused an increase in channel stability. This has allowed encroachment of the river by exotic vegetation, and a reduction in the width of the un-vegetated fairway, by 250 m in the Duntroon area (Meridian Energy 2003). Over the same time period the rivers has changed from braiding to anastomosing, with fewer individual channels, which are more stable in their location (Bravard and Gilvear 1996, Meridian Energy 2003). Figure 3 illustrates the simulated effect of continued vegetation encroachment in the absence of sediment input and bed-load moving flood events. The lower Waitaki is no longer a braided river system and as a result there has been a drastic reduction in flood plain area, habitat heterogeneity, ecosystem and physical services provided by the river, and the loss of species adapted to life within the shifting habitat mosaic (Meridian Energy

2003). Although groundwater fed channels were recorded in the lower Waitaki during 2003, the long term effects of system in-balance on these habitats are unknown.

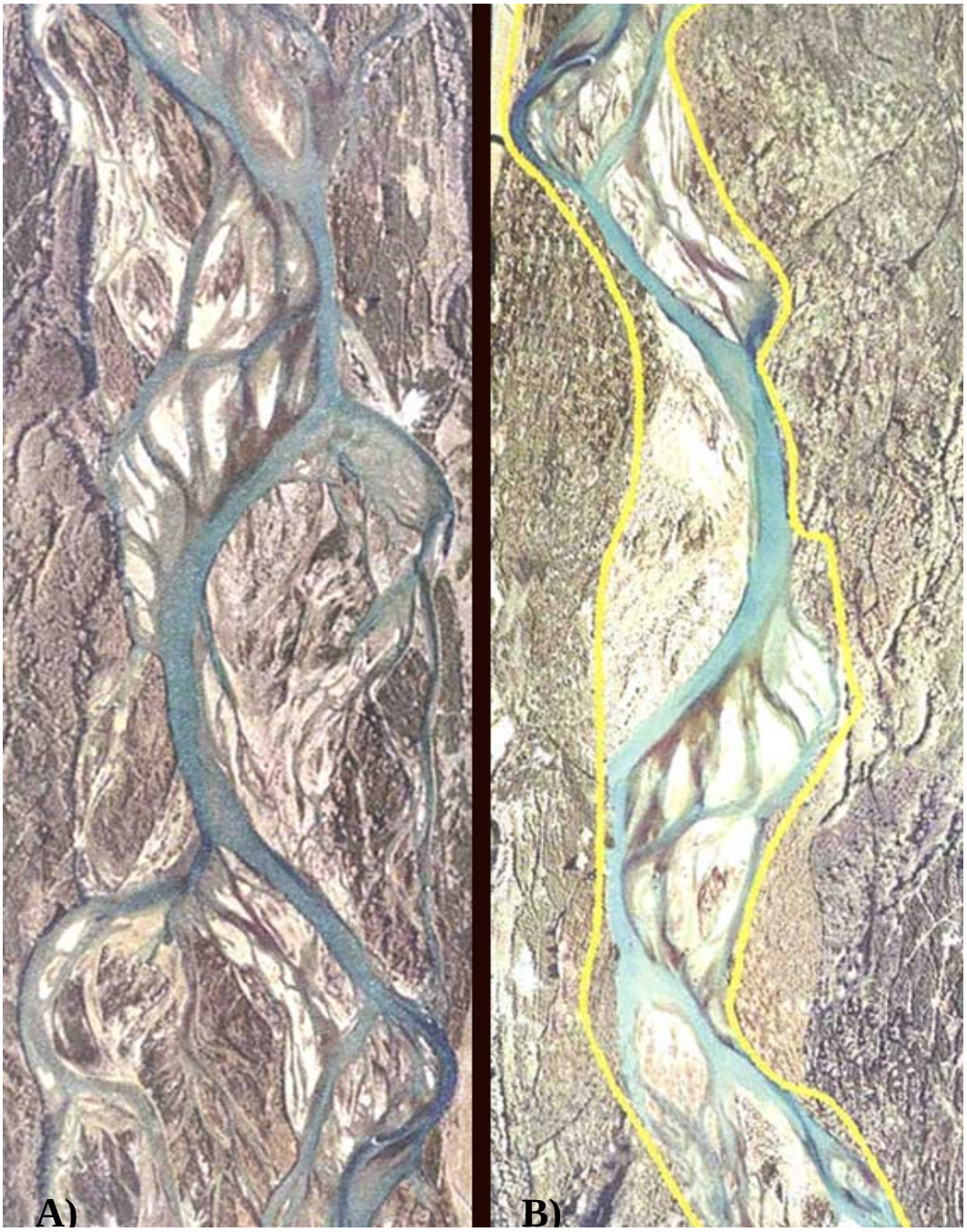

Figure 3. A) Aerial photograph of the Waitaki River (July 2001). B) Simulated aerial view of how the river might look in 30 years if vegetation encroachment is allowed to continue. (Meridian Energy 2003).

The effect on springs of river impoundment is context dependent. Ward and Stanford (1995) described a situation where a reduction in sediment load resulted in bed incision and a lowering of the flood plain water table, which resulted in the draining of wetlands. Conversely, Brunke (2002) recorded a reduction in surface connectivity on the dammed, channelised and water-abstracted Brenno River, in Switzerland. However, vertical connectivity remained, and exfiltration of groundwater maintained the integrity of remnant aquatic flood plain habitats.

Achieving a balance between societal needs for power generation, water management/use and land uses, and maintaining the ecological integrity of riverine landscapes, such as spring complexes, is the challenge faced by river managers (Ward et al. 2002, Hauer and Lorang 2004). The upper Snake River in eastern Idaho has been damned for hydroelectricity generation, resulting in altered flow regimes and decreased sediment load. Hauer and Lorang (2004) used aerial photography and ground based measurements to estimate hydrographic regimes required to cause bed and riparian sediment movement. These thresholds were required to re-establish the "shifting habitat mosaic"(SHM) historically characteristic of flood plain reaches on the Snake River. However, the long term efficacy and sustainability of hydrologic manipulation capable of maintaining a SHM in the absence of sediment addition from headwaters, is a moot point.

6.4 Conclusion

Springs in braided river beds and their fauna are dependent on the spatial and temporal dynamic equilibrium of flood plain elements, and connectivity within the braided river flood plain. Biodiversity is maintained by the heterogeneity of

connectedness and by successional stage, both of which are kept in more-or-less constant proportions by the natural flow regime driven, adherence to a shifting mosaic steady state model (Arscott et al. 2002, van der Nat et al. 2003, Hauer and Lorang 2004).

Anthropogenic activities such as diversion, channelisation and impoundment can have severe impacts upon this balance. Consideration of the bio-diversity values of a river system must take into account habitat diversity and functional integrity of the whole system from source to the sea (Pringle 1997, Ward et al. 1999b, Pringle 2001). The river is an integral part of the landscape and is as much defined by it, as it has the power to shape it. More specifically, flood plain reaches are a feature of many glacially derived river valleys within New Zealand, and globally. In order to maintain the collective integrity of the physically and biologically disparate habitats found within these river corridors, a holistic management approach is required. The statement "look after the springs and you look after the river" (Kilroy et al. 2004), is in accordance with Stanford's (1998) expanded three-dimensional view of the "river". The findings of my study reassert these axioms by highlighting the value of springs as hotspots of biodiversity within the wider riverine landscape.

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Appendix 1

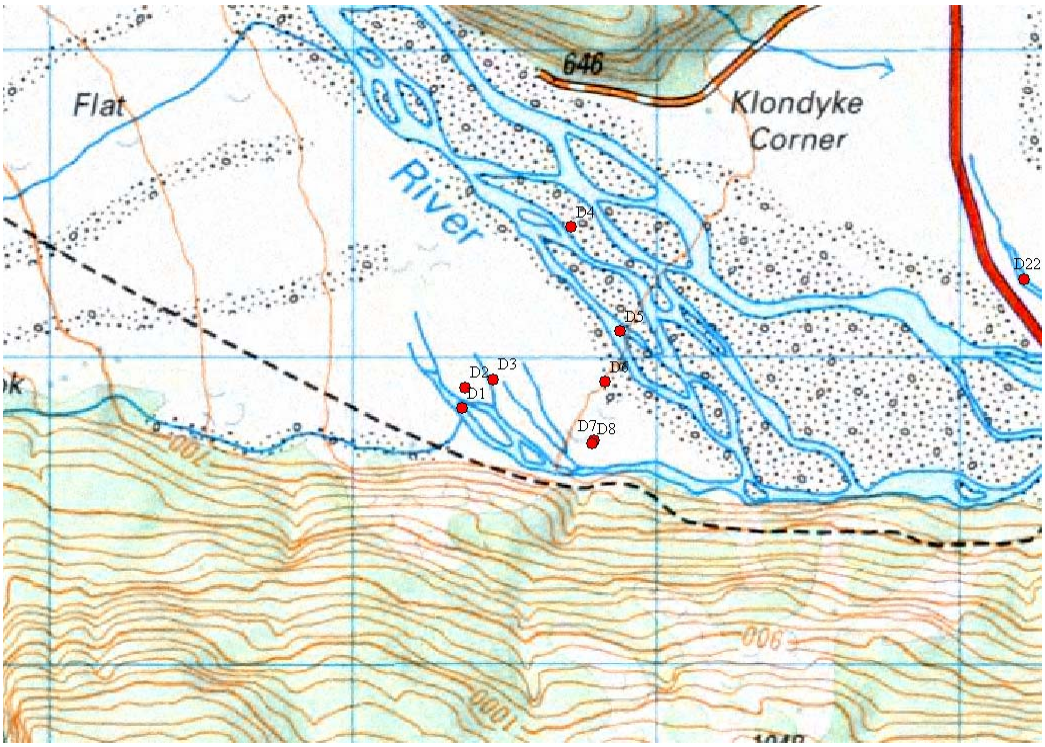
Spring and main channel sampling site locations and characteristics

			New Zealand map grid				
Type	**Location**	**Site no**	**Easting**	**Northing**	**Species richness**	**Sites age**	**Mean discharge**
Spring	Turkey fan	1	2393353	5797834	26	4	0.159
Spring	Turkey fan	2	2393365	5797902	21	5	0.657
Spring	Turkey fan	3	2393458	5797928	20	5	0.255
Main channel	Turkey fan	4	2393715	5798423	14	1	
Spring	Turkey fan	5	2393874	5798084	12	2	0.050
Spring	Turkey fan	6	2393830	5797930	13	3	0.006
Spring	Turkey fan	7	2393789	5797728	24	5	0.107
Spring	Turkey fan	8	2393783	5797718	26	5	0.047
Hill slope	Turkey fan		2393760	5797595	17		0.018
Spring	O'Malleys flat	9	2398769	5798691	20	4	0.067
Spring	O'Malleys flat	10	2398509	5798754	27	5	0.049
Spring	O'Malleys flat	11	2398423	5798766	18	5	0.064
Spring	O'Malleys flat	12	2398501	5798632	23	4	0.095
Main channel	O'Malleys flat	13	2398544	5798277	13	1	
Spring	O'Malleys flat	14	2398473	5798327	Wash out	1	
Spring	O'Malleys flat	15	2398328	5798827	12	5	0.096
Hill slope	O'Malleys flat		2397780	5799395	16		0.016
Spring	Klondyke	16	2396012	5797840	20	3	0.011
Main channel	Klondyke	17	2396076	5797657	13	1	
Spring	Klondyke	18	2395948	5797717	13	1	0.382
Spring	Klondyke	19	2396216	5797939	12	3	0.006
Spring	Klondyke	20	2395839	5798036	13	3	0.093
Spring	Klondyke	21	2395792	5798067	17	4	0.117
Spring	Klondyke	22	2395205	5798254	12	4	0.316
Hill slope	Klondyke		2394435	5799185	25		0.002
Spring	Cora Lyn	23	2402509	5796817	23	3	0.039
Spring	Cora Lyn	24	2403479	5797336	19	4	0.016
Spring	Cora Lyn	25	2403474	5797408	18	4	0.061
Spring	Cora Lyn	26	2403599	5797761	17	3	0.068
Main channel	Cora Lyn	27	2403424	5798399	12	1	
Spring	Cora Lyn	28	2403031	5796918	29	5	0.078
Spring	Cora Lyn	29	2402649	5796711	21	5	0.133
Hill slope	Cora Lyn		2402855	5796805	22		0.013
Spring	One Tree Swamp	30	2406545	5800136	22	5	
Spring	One Tree Swamp	31	2406043	5800103	22	5	0.146
Spring	One Tree Swamp	32	2405862	5799911	22	5	0.153
Main channel	One Tree Swamp	33	2406303	5799665	14	1	
Spring	One Tree Swamp	34	2406323	5799785	23	2	0.196
Spring	One Tree Swamp	35	2406343	5799903	20	5	0.235
Spring	One Tree Swamp	36	2406555	5800042	16	5	0.013
Hill slope	One Tree Swamp		2402855	5796805	19		0.003
Spring	Waimak Spring	37	2413051	5798469	18	4	0.021
Spring	Waimak Spring	38	2412961	5798488	22	4	0.018
Spring	Waimak Spring	39	2412628	5798512	30	2	0.138
Main channel	Waimak Spring	40	2412424	5798390	17	1	
Spring	Waimak Spring	41	2412212	5798831	20	3	0.026
Spring	Waimak Spring	42	2412951	5798499	30	5	0.095
Hill slope	Waimak Spring		2412795	5799115	22		0.078
Spring	Hawdon Valley	43	2407735	5803742	30	5	0.050

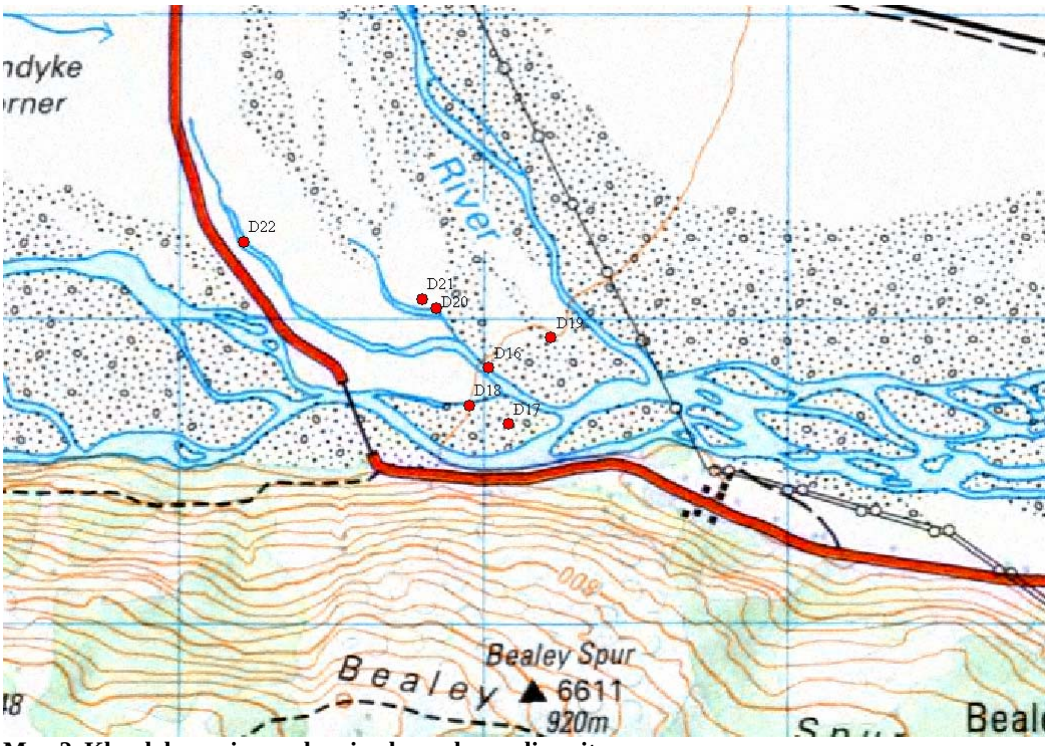
Spring	Hawdon Valley	44	2407797	5803790	23	5	0.042
Spring	Hawdon Valley	45	2407827	5803765	25	4	0.048
Spring	Hawdon Valley	46	2407875	5803761	24	3	0.031
Spring	Hawdon Valley	47	2407999	5803852	14	3	0.022
Spring	Hawdon Valley	48	2408221	5803935	19	2	0.030
Main channel	Hawdon Valley	49	2408323	5803910	12	1	
Hill slope	Hawdon Valley		2408495	5803515	22		0.043

Appendix 2

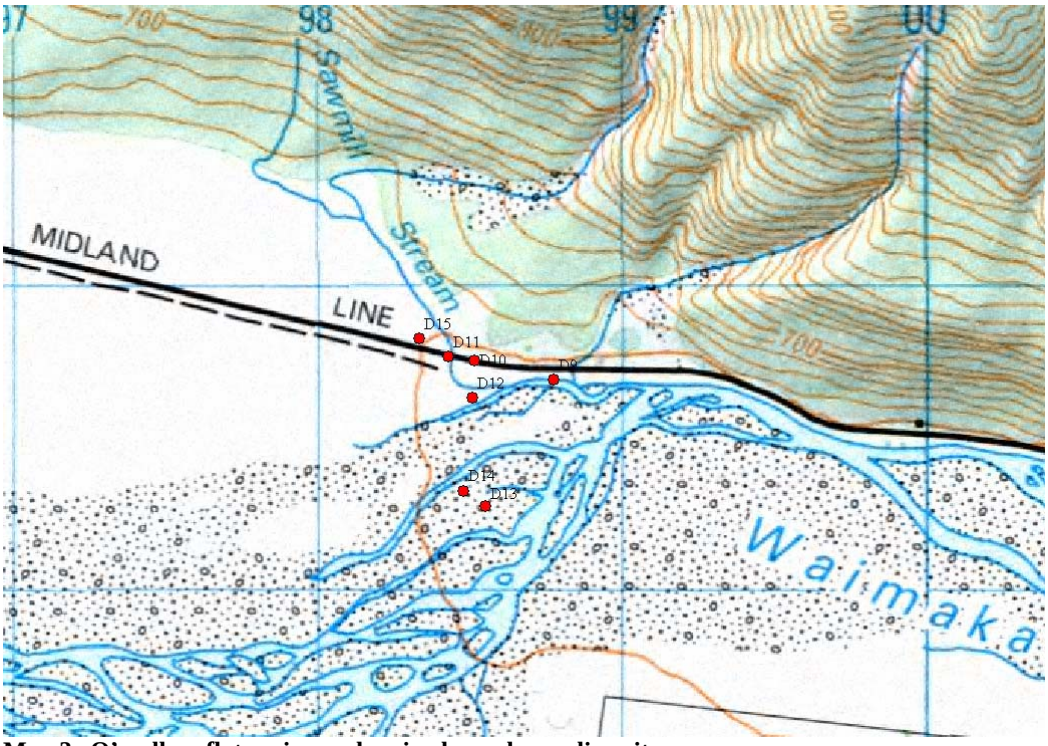
Sampling site maps for spring and main channel sites (Chapter 3 & 4).



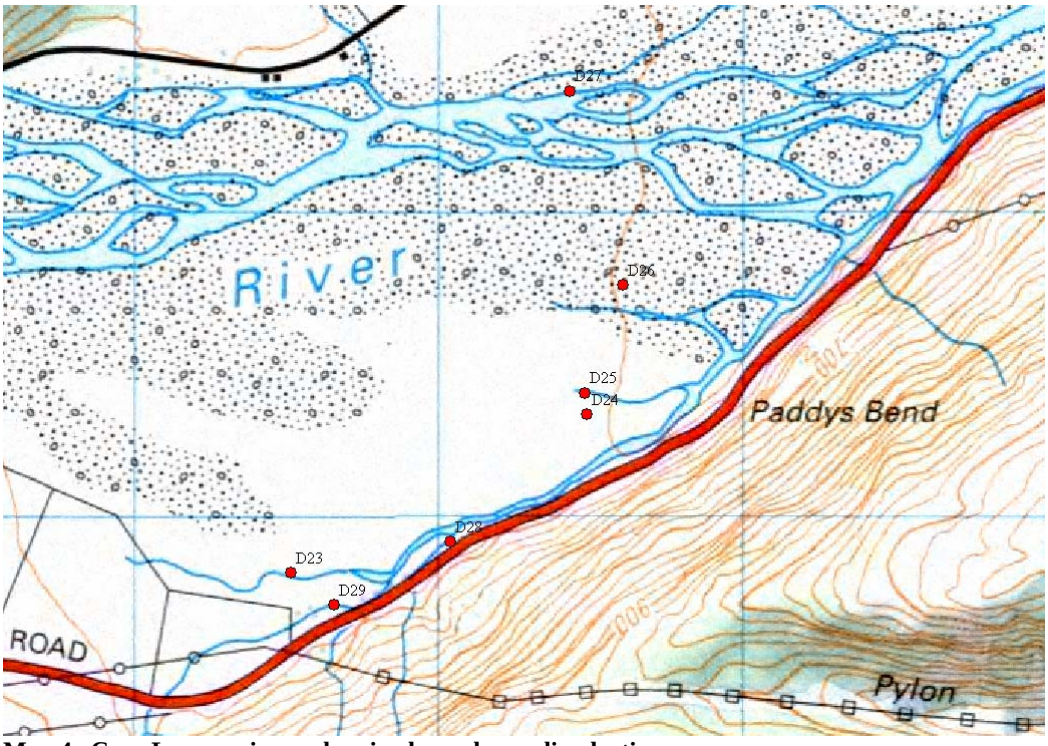
Map 1. Turkey fan spring and main channel sampling sites. Numbers correspond to sites listed in appendix 1 and described in the text.



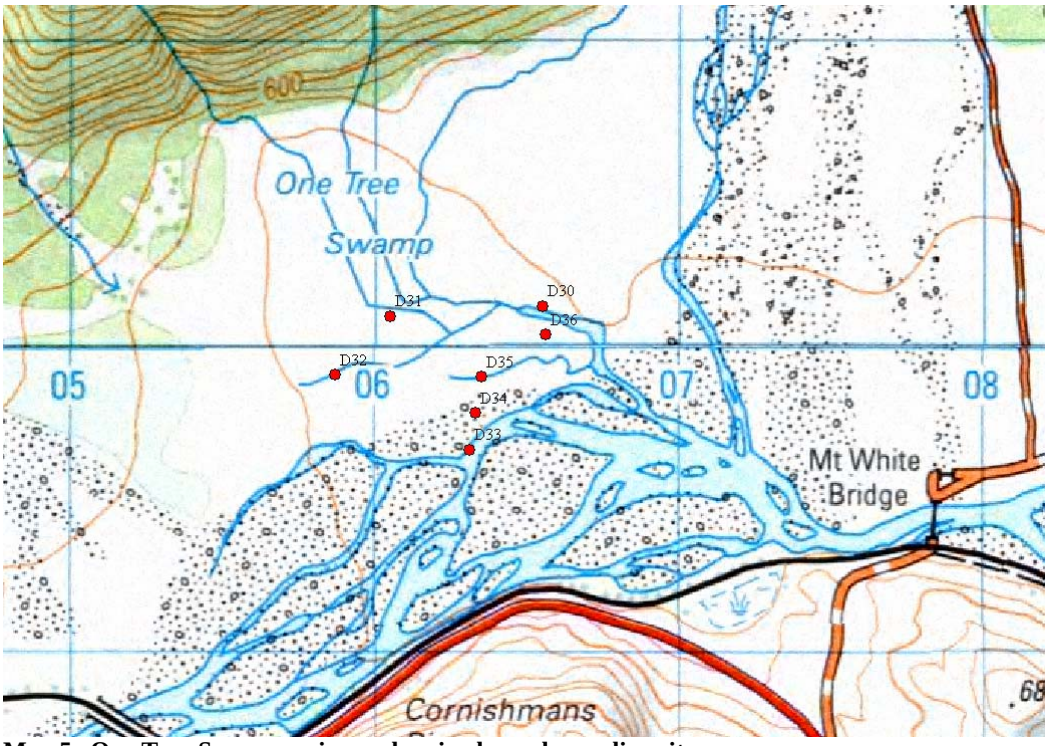
Map 2. Klondyke spring and main channel sampling sites.



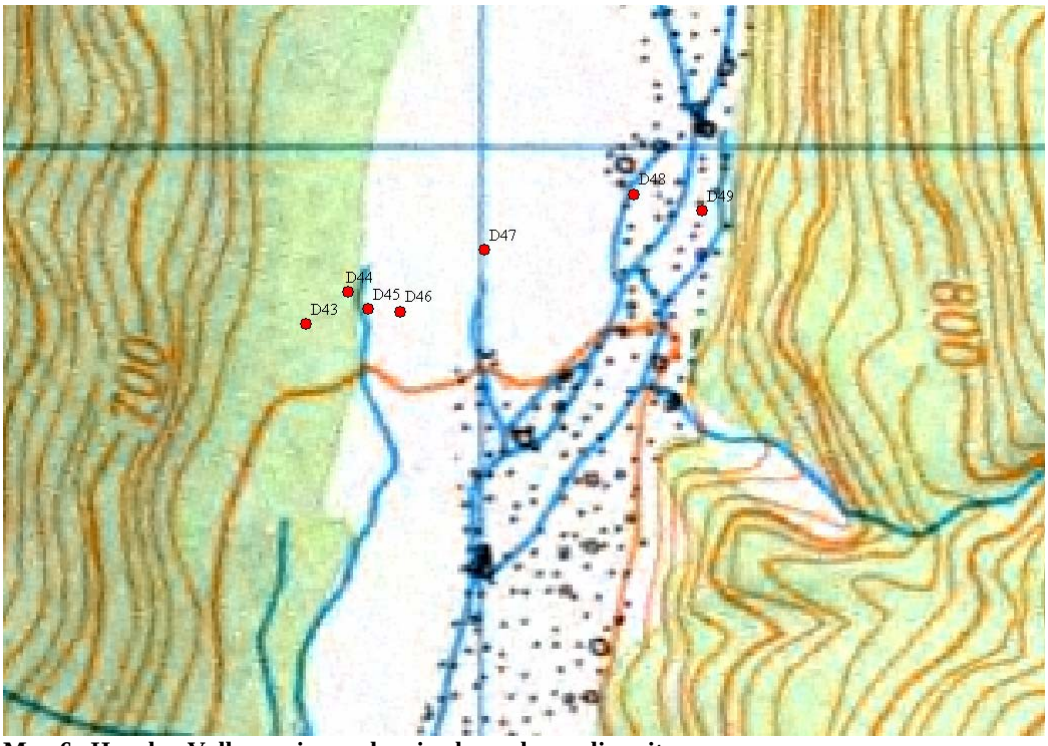
Map 3. O'malleys flat spring and main channel sampling sites.



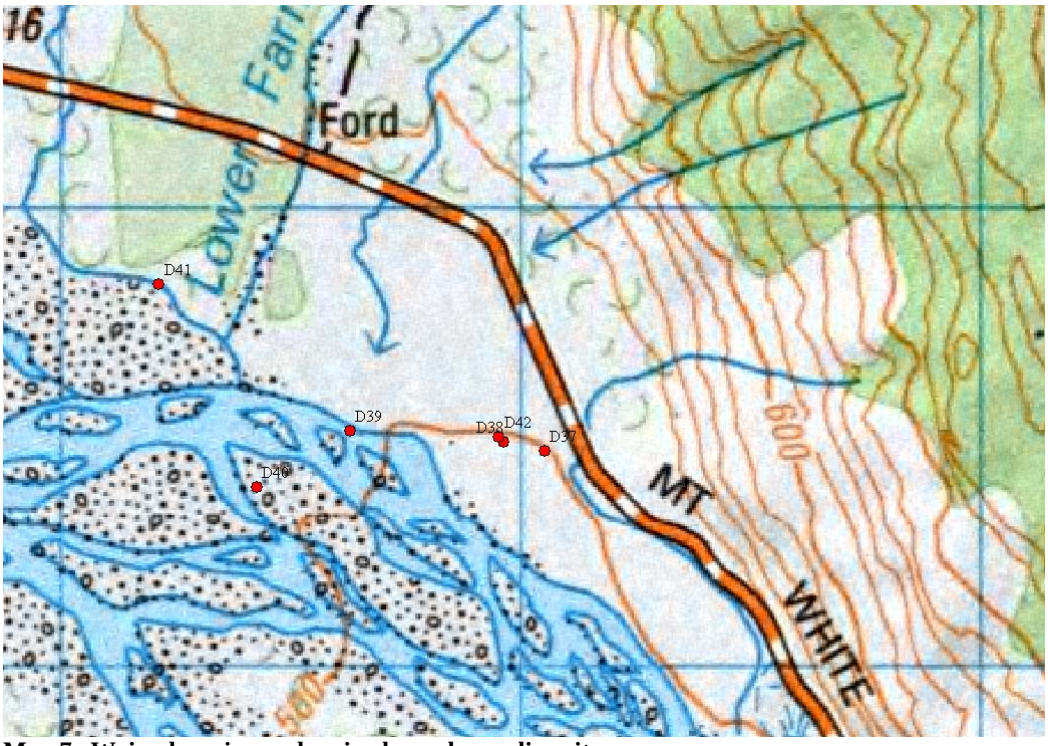
Map 4. Cora Lynn spring and main channel sampling loctions



Map 5. One Tree Swamp spring and main channel sampling sites.



Map 6. Hawdon Valley spring and main channel sampling sites.



Map 7. Waimak spring and main channel sampling sites.

Appendix 3

Invertebrate data for all sites, averaged over both sampling occasions.
Functional feeding groups;
Cb = Collector browsers
P = Predators
F = Filter feeders
Hp = Piercer
Sh = shredder
Sc = scrapper

Appendix 3

Taxa	*ffg*	Turkey 1	Turkey 2	Turkey 3	Turkey 4	Turkey 5
Nannochorista philpotti	*p*	0	0	0	0	0
Kempynus sp.	*p*	0	0	0	0	1
Coloburiscus humeralis	*f*	0	0	0	0	0
Nesameletus ornatus	*cb*	1	1	0	0	0
Nesameletus austrinus	*cb*	0	0	0	0	0
Oniscigaster wakefieldi	*cb*	0	0	0	0	0
Austroclima sp.	*cb*	0	0	0	0	0
Deleatidium spp.	*cb*	60	3	51	100	0
Austroperla cyrene	*sh*	0	0	0	0	0
Stenaperla maclellani	*p*	1	0	0	0	0
Taraperla howsei	*cb*	0	0	0	0	0
Zelandoperla sp.	*cb*	1	0	3	5	0
Zelandobius unicolor	*cb*	10	3	10	0	0
Zelandobius pilosus	*cb*	0	0	1	0	0
Zelandobius confusus	*cb*	0	0	1	0	0
Zelandobius furcillatus	*cb*	5	3	10	3	0
Cristaperla sp.	*cb*	0	0	0	0	0
Spaniocerca sp.	*cb*	0	0	0	0	0
Megaleptoperla grandis	*p*	0	0	0	0	0
Halticoperla viridans	*cb*	0	0	0	0	0
Aoteapsyche colonica	*f*	0	0	0	0	0
Beraeoptera roria	*cb*	0	0	0	0	0
Oxyethira sp.	*hp*	3	1	3	0	1
Paroxyethira eatoni	*hp*	0	10	0	0	0
Psilochorema sp.	*p*	0	0	0	0	0
Olinga feredayi	*cb*	0	0	0	0	0
Hydrobiosidae indent.	*p*	1	1	1	1	1
Hydrobiosis charadraea	*p*	0	0	0	1	0
Hydrobiosis clavigera	*p*	0	0	0	0	0
Hydrobiosis parumbripennis	*p*	1	3	1	0	0
Hydrobiosis torrentis	*p*	0	0	0	1	0
Hydrobiosis soro	*p*	0	0	0	0	0
Hydrobiosis neadelphus (styx)	*p*	0	0	0	0	0
Hydrobiosis silvicola-gp	*p*	0	0	0	0	0
Hydrobiosis chalcodes	*p*	3	1	0	0	0
Hydrobiosis harpidiosa	*p*	0	0	0	0	0
Costachorema xanthopterum	*p*	0	0	0	0	0
Polyplectropus sp.	*p*	0	0	0	0	0
Philorheithrus agilis	*p*	0	0	0	0	0
Oeconesus sp.	*cb*	0	1	0	0	0
Hudsonema amabile	*p*	0	0	0	0	0
Hudsonema alienium	*p*	0	0	0	0	0
Triplectides obsoletus	*sh*	0	0	0	0	0
Pycnocentrodes sp.	*cb*	0	5	1	0	0
Pycnocentria funerea	*cb*	0	0	0	0	0
Pycnocentria evecta	*cb*	0	3	3	0	0
Edpercivalia sp.	*p*	0	0	0	0	0

Hydrobiosella sp.	*f*	0	0	0	0	0
Hydrochorema tenuicaudatum	*p*	0	0	0	0	0
Trailochorema	p	0	0	0	0	0
Costachorema psaropterum	*p*	0	0	0	0	0
Pycnocentria sylvestris	*cb*	0	0	0	0	0
Zealandopsyche ingens	*sh*	0	0	0	0	0
Ocetis unicolor	*p*	0	0	0	0	0
Zellolisica cheira	*cb*	0	0	0	0	0
Scirtidae	*cb*	1	0	1	0	1
Huxelhydrus syntheticus	*p*	0	0	0	0	0
Antiporus stigosulus	*p*	0	0	0	0	1
Liodessus deflectus	*p*	0	0	0	0	0
Hydrophilidae	*p*	0	0	0	1	0
Antiporus femoralis	p	0	0	0	0	0
Ptilodactylidae	*cb*	1	0	0	0	0
Hydraenidae	*sh*	0	0	0	0	0
Elmidae	*cb*	0	0	0	1	1
Hexatomini sp.	*cb*	0	0	0	0	0
Psychodidae	*cb*	0	0	0	0	0
Ceratopogonidae	*p*	1	0	0	0	0
Sciomyzidae	*p*	0	0	0	0	0
Limonia sp.	*sh*	0	0	1	0	0
Muscidae	*cb*	3	1	0	0	3
Aphrophila sp.	*cb*	0	0	0	1	0
Zelandotipula sp.	*cb*	1	0	0	0	0
Tabanidae	*p*	0	0	0	0	0
Eriopterini	*cb*	1	0	1	1	3
Neocurupira	*sc*	0	0	0	1	0
Stradiomyidae	*cb*	1	0	0	0	0
Empididae	*cb*	1	0	0	0	0
culex	*f*	0	0	0	0	0
Nothodixa	*cb*	0	0	0	0	0
Austrosimulium	*f*	3	0	1	1	10
Tanypodinae	*p*	1	13	0	1	1
Chironominae	*cb*	0	0	0	0	0
Diamesinae	*cb*	5	0	50	0	10
Orthocladiinae	*cb*	5	5	13	3	10
Potamopyrgus antipodarum	*sc*	10	20	51	0	0
Sphaeriadae	*f*	0	0	0	0	0
Lymnae tomentosa	*sc*	0	3	0	0	0
Phreatogammerus sp.	*cb*	0	1	0	0	0
Paraleptamphopus sp.	*cb*	1	1	0	0	0
Ostracod	*f*	0	3	0	0	0
Turbellaria	*p*	5	3	1	0	0
Prorhynchus putealis	*p*	0	0	1	0	0
Hirudinae	*p*	0	0	0	0	0
Acari	*p*	0	0	0	0	0
Oniscoidea	*cb*	0	0	0	0	0
Oligochaeta	*cb*	3	0	0	0	0
Nematomorpha		0	0	0	0	0

Archicauliodes diversus	*p*	0	0	0	0	0
Sigara sp.	hp	0	0	0	0	0

Taxa	***ffg***	**Turkey 6**	**Turkey 7**	**Turkey 8**	**Turkey hill**	**O'Malleys 9**
Nannochorista philpotti	*p*	0	0	0	0	0
Kempynus sp.	*p*	0	0	0	0	0
Coloburiscus humeralis	*f*	0	0	0	0	0
Nesameletus ornatus	*cb*	0	0	0	0	0
Nesameletus austrinus	*cb*	0	0	0	10	0
Oniscigaster wakefieldi	*cb*	0	0	0	0	0
Austroclima sp.	*cb*	0	0	0	0	0
Deleatidium spp.	*cb*	0	11	3	50	53
Austroperla cyrene	*sh*	0	0	0	0	1
Stenaperla maclellani	*p*	0	0	0	1	0
Taraperla howsei	*cb*	0	0	0	1	0
Zelandoperla sp.	*cb*	0	0	0	3	0
Zelandobius unicolor	*cb*	0	0	0	10	0
Zelandobius pilosus	*cb*	0	1	0	0	0
Zelandobius confusus	*cb*	0	0	0	0	0
Zelandobius furcillatus	*cb*	0	0	0	3	5
Cristaperla sp.	*cb*	0	0	0	0	0
Spaniocerca sp.	*cb*	0	0	0	1	0
Megaleptoperla grandis	*p*	0	0	0	0	0
Halticoperla viridans	*cb*	0	0	0	0	0
Aoteapsyche colonica	*f*	0	0	0	0	0
Beraeoptera roria	*cb*	0	0	0	0	0
Oxyethira sp.	*hp*	1	1	1	0	0
Paroxyethira eatoni	*hp*	0	0	3	0	0
Psilochorema sp.	*p*	0	10	1	0	1
Olinga feredayi	*cb*	0	0	0	3	0
Hydrobiosidae indent.	*p*	0	1	1	0	1
Hydrobiosis charadraea	*p*	0	0	0	0	0
Hydrobiosis clavigera	*p*	0	0	0	0	0
Hydrobiosis parumbripennis	*p*	0	5	3	0	3
Hydrobiosis torrentis	*p*	0	0	0	0	0
Hydrobiosis soro	*p*	0	0	0	0	0
Hydrobiosis neadelphus (styx)	*p*	0	0	0	0	0
Hydrobiosis silvicola-gp	*p*	0	0	0	3	0
Hydrobiosis chalcodes	*p*	0	0	1	0	0
Hydrobiosis harpidiosa	*p*	0	0	0	0	0
Costachorema xanthopterum	*p*	0	0	0	0	0
Polyplectropus sp.	*p*	0	0	0	0	0
Philorheithrus agilis	*p*	0	0	0	0	0
Oeconesus sp.	*cb*	0	0	1	0	0
Hudsonema amabile	*p*	0	0	0	0	0
Hudsonema alienium	*p*	0	0	0	0	0
Triplectides obsoletus	*sh*	0	0	0	0	0
Pycnocentrodes sp.	*cb*	1	13	53	0	13
Pycnocentria funerea	*cb*	0	50	1	0	53

Pycnocentria evecta	*cb*	0	53	250	0	10
Edpercivalia sp.	*p*	0	0	0	1	0
Hydrobiosella sp.	*f*	0	0	0	3	0
Hydrochorema tenuicaudatum	*p*	0	0	0	3	0
Trailochorema	p	0	0	0	0	0
Costachorema psaropterum	*p*	0	0	0	0	1
Pycnocentria sylvestris	*cb*	0	0	0	0	0
Zealandopsyche ingens	*sh*	0	0	0	0	0
Ocetis unicolor	*p*	0	0	0	0	0
Zellolisica cheira	*cb*	0	0	0	0	0
Scirtidae	*cb*	1	1	0	0	0
Huxelhydrus syntheticus	*p*	50	0	0	0	0
Antiporus stigosulus	*p*	3	0	0	0	0
Liodessus deflectus	*p*	0	0	0	0	0
Hydrophilidae	*p*	0	0	0	0	0
Antiporus femoralis	p	0	0	0	0	0
Ptilodactylidae	*cb*	0	0	0	0	0
Hydraenidae	*sh*	0	0	0	0	0
Elmidae	*cb*	1	0	0	1	0
Hexatomini sp.	*cb*	0	0	0	0	0
Psychodidae	*cb*	0	0	1	0	0
Ceratopogonidae	*p*	0	1	0	0	0
Sciomyzidae	*p*	0	0	1	0	0
Limonia sp.	*sh*	1	3	1	0	1
Muscidae	*cb*	1	3	1	0	1
Aphrophila sp.	*cb*	0	0	0	0	1
Zelandotipula sp.	*cb*	0	0	1	0	3
Tabanidae	*p*	0	0	0	0	0
Eriopterini	*cb*	1	0	0	1	0
Neocurupira	*sc*	0	0	0	0	0
Stradiomyidae	*cb*	1	0	0	0	0
Empididae	*cb*	0	0	0	0	0
culex	*f*	1	0	0	0	0
Nothodixa	*cb*	0	0	0	0	0
A*ustrosimulium*	*f*	0	0	0	1	0
Tanypodinae	*p*	0	1	5	0	1
Chironominae	*cb*	3	1	3	0	0
Diamesinae	*cb*	0	10	50	0	10
Orthocladiinae	*cb*	0	53	60	3	20
Potamopyrgus antipodarum	*sc*	0	20	250	0	53
Sphaeriadae	*f*	0	0	0	0	0
Lymnae tomentosa	*sc*	0	0	0	0	0
Phreatogammerus sp.	*cb*	0	1	0	0	0
Paraleptamphopus sp.	*cb*	1	1	1	0	1
Ostracod	*f*	0	50	10	0	0
Turbellaria	*p*	0	11	3	0	3
Prorhynchus putealis	*p*	0	1	1	0	0
Hirudinae	*p*	0	0	0	0	0
Acari	*p*	0	1	3	0	0
Oniscoidea	*cb*	0	0	0	0	0

Oligochaeta	*cb*	0	0	0	0	0
Nematomorpha		0	0	0	0	0
Archicauliodes diversus	*p*	0	0	0	0	0
Sigara sp.	hp	0	0	0	0	0

Taxa	***ffg***	**O'Malleys 10**	**O'Malleys 11**	**O'Malleys 12**	**O'Malleys 13**	**O'Malleys 14**
Nannochorista philpotti	*p*	0	0	0	0	0
Kempynus sp.	*p*	0	0	0	0	0
Coloburiscus humeralis	*f*	0	0	0	0	0
Nesameletus ornatus	*cb*	1	0	0	0	0
Nesameletus austrinus	*cb*	0	0	0	0	0
Oniscigaster wakefieldi	*cb*	0	0	0	0	0
Austroclima sp.	*cb*	0	0	0	0	0
Deleatidium spp.	*cb*	5	20	20	20	0
Austroperla cyrene	*sh*	5	1	0	0	0
Stenaperla maclellani	*p*	0	0	0	0	0
Taraperla howsei	*cb*	0	0	0	0	0
Zelandoperla sp.	*cb*	0	0	5	3	0
Zelandobius unicolor	*cb*	0	1	3	0	0
Zelandobius pilosus	*cb*	0	0	0	0	0
Zelandobius confusus	*cb*	0	0	1	0	0
Zelandobius furcillatus	*cb*	5	0	13	3	0
Cristaperla sp.	*cb*	0	0	0	0	0
Spaniocerca sp.	*cb*	0	0	0	0	0
Megaleptoperla grandis	*p*	1	0	0	0	0
Halticoperla viridans	*cb*	0	0	0	0	0
Aoteapsyche colonica	*f*	0	0	0	0	0
Beraeoptera roria	*cb*	0	0	0	0	0
Oxyethira sp.	*hp*	3	0	1	0	0
Paroxyethira eatoni	*hp*	1	0	0	0	0
Psilochorema sp.	*p*	1	3	1	1	0
Olinga feredayi	*cb*	0	0	0	0	0
Hydrobiosidae indent.	*p*	0	3	1	0	0
Hydrobiosis charadraea	*p*	0	0	0	0	0
Hydrobiosis clavigera	*p*	0	0	0	0	0
Hydrobiosis parumbripennis	*p*	3	3	3	0	0
Hydrobiosis torrentis	*p*	0	0	0	0	0
Hydrobiosis soro	*p*	0	0	0	0	0
Hydrobiosis neadelphus (styx)	*p*	0	0	0	0	0
Hydrobiosis silvicola-gp	*p*	0	0	0	0	0
Hydrobiosis chalcodes	*p*	0	0	1	0	0
Hydrobiosis harpidiosa	*p*	0	0	0	1	0
Costachorema xanthopterum	*p*	0	0	0	0	0
Polyplectropus sp.	*p*	0	0	0	0	0
Philorheithrus agilis	*p*	0	0	0	0	0
Oeconesus sp.	*cb*	0	0	0	0	0
Hudsonema amabile	*p*	1	0	0	0	0
Hudsonema alienium	*p*	0	0	0	0	0
Triplectides obsoletus	*sh*	0	0	0	0	0

Pycnocentrodes sp.	*cb*	3	5	5	0	0
Pycnocentria funerea	*cb*	0	0	0	0	0
Pycnocentria evecta	*cb*	0	0	0	0	0
Edpercivalia sp.	*p*	0	0	0	0	0
Hydrobiosella sp.	*f*	0	0	0	0	0
Hydrochorema tenuicaudatum	*p*	0	0	0	0	0
Trailochorema	p	0	0	0	1	0
Costachorema psaropterum	*p*	0	0	0	0	0
Pycnocentria sylvestris	*cb*	3	0	0	0	0
Zealandopsyche ingens	*sh*	0	0	0	0	0
Ocetis unicolor	*p*	0	0	0	0	0
Zellolisica cheira	*cb*	0	0	1	0	0
Scirtidae	*cb*	3	1	0	0	0
Huxelhydrus syntheticus	*p*	0	0	0	0	0
Antiporus stigosulus	*p*	0	0	0	0	0
Liodessus deflectus	*p*	1	0	0	0	0
Hydrophilidae	*p*	0	0	0	0	0
Antiporus femoralis	p	0	0	0	0	0
Ptilodactylidae	*cb*	0	0	0	0	0
Hydraenidae	*sh*	0	0	0	0	0
Elmidae	*cb*	0	1	1	3	0
Hexatomini sp.	*cb*	0	0	0	0	0
Psychodidae	*cb*	0	0	0	0	0
Ceratopogonidae	*p*	1	0	1	1	0
Sciomyzidae	*p*	0	0	0	0	0
Limonia sp.	*sh*	3	5	1	0	0
Muscidae	*cb*	1	3	1	1	0
Aphrophila sp.	*cb*	0	0	0	0	0
Zelandotipula sp.	*cb*	0	0	0	0	0
Tabanidae	*p*	0	0	0	0	0
Eriopterini	*cb*	0	0	0	3	0
N*eocurupira*	*sc*	0	0	0	0	0
Stradiomyidae	*cb*	1	0	0	0	0
Empididae	*cb*	1	0	0	0	0
culex	*f*	0	0	0	0	0
Nothodixa	*cb*	0	0	0	0	0
Austrosimulium	*f*	0	3	10	0	0
Tanypodinae	*p*	3	0	1	0	0
Chironominae	*cb*	0	0	0	0	0
Diamesinae	*cb*	5	3	10	3	0
Orthocladiinae	*cb*	11	5	1	1	0
Potamopyrgus antipodarum	*sc*	3	3	11	0	0
Sphaeriadae	*f*	0	0	0	0	0
Lymnae tomentosa	*sc*	0	0	0	0	0
Phreatogammerus sp.	*cb*	0	0	0	1	0
Paraleptamphopus sp.	*cb*	13	20	1	0	0
Ostracod	*f*	0	0	0	0	0
Turbellaria	*p*	5	5	3	0	0
Prorhynchus putealis	*p*	1	0	0	0	0
Hirudinae	*p*	0	0	0	0	0

Acari	*p*	0	0	0	0	0
Oniscoidea	*cb*	0	1	0	0	0
Oligochaeta	*cb*	1	0	0	0	0
Nematomorpha		0	0	0	0	0
Archicauliodes diversus	*p*	0	0	0	0	0
Sigara sp.	hp	0	0	0	0	0

Taxa	***ffg***	**O'Malleys 15**	**O'malleys hill**	**Klondyke 16**	**Klondyke 17**	**Klondyke 18**
Nannochorista philpotti	*p*	0	0	0	0	0
Kempynus sp.	*p*	0	0	0	0	0
Coloburiscus humeralis	*f*	0	3	0	0	0
Nesameletus ornatus	*cb*	1	0	3	0	13
Nesameletus austrinus	*cb*	0	10	0	0	0
Oniscigaster wakefieldi	*cb*	0	0	0	0	0
Austroclima sp.	*cb*	0	0	0	0	0
Deleatidium spp.	*cb*	13	50	3	100	100
Austroperla cyrene	*sh*	0	0	0	0	0
Stenaperla maclellani	*p*	0	0	0	0	0
Taraperla howsei	*cb*	0	0	0	0	0
Zelandoperla sp.	*cb*	0	10	0	1	1
Zelandobius unicolor	*cb*	0	0	0	3	1
Zelandobius pilosus	*cb*	0	0	0	0	0
Zelandobius confusus	*cb*	0	0	0	0	0
Zelandobius furcillatus	*cb*	0	10	0	10	1
Cristaperla sp.	*cb*	0	0	0	0	0
Spaniocerca sp.	*cb*	0	3	0	0	0
Megaleptoperla grandis	*p*	0	0	0	0	0
Halticoperla viridans	*cb*	0	0	0	0	0
Aoteapsyche colonica	*f*	0	3	0	0	0
Beraeoptera roria	*cb*	0	0	0	0	0
Oxyethira sp.	*hp*	0	0	13	0	0
Paroxyethira eatoni	*hp*	0	0	0	0	0
Psilochorema sp.	*p*	0	3	1	0	0
Olinga feredayi	*cb*	0	0	0	0	0
Hydrobiosidae indent.	*p*	0	1	0	1	1
Hydrobiosis charadraea	*p*	0	0	0	0	0
Hydrobiosis clavigera	*p*	0	0	0	0	0
Hydrobiosis parumbripennis	*p*	1	0	0	1	0
Hydrobiosis torrentis	*p*	0	0	0	0	0
Hydrobiosis soro	*p*	0	0	0	0	0
Hydrobiosis neadelphus (styx)	*p*	0	3	0	0	0
Hydrobiosis silvicola-gp	*p*	0	3	0	0	0
Hydrobiosis chalcodes	*p*	0	0	0	0	0
Hydrobiosis harpidiosa	*p*	0	0	0	0	0
Costachorema xanthopterum	*p*	0	0	0	0	0
Polyplectropus sp.	*p*	0	0	0	0	0
Philorheithrus agilis	*p*	0	0	0	0	0
Oeconesus sp.	*cb*	0	0	0	0	0
Hudsonema amabile	*p*	0	0	3	0	0

Hudsonema alienium	*p*	0	0	1	0	0
Triplectides obsoletus	*sh*	0	0	0	0	0
Pycnocentrodes sp.	*cb*	0	0	11	3	0
Pycnocentria funerea	*cb*	0	0	0	0	0
Pycnocentria evecta	*cb*	0	0	0	0	0
Edpercivalia sp.	*p*	0	0	0	0	0
Hydrobiosella sp.	*f*	0	0	0	0	0
Hydrochorema tenuicaudatum	*p*	0	0	0	0	0
Trailochorema	p	0	0	0	0	1
Costachorema psaropterum	*p*	0	0	0	0	0
Pycnocentria sylvestris	*cb*	0	0	0	0	0
Zealandopsyche ingens	*sh*	0	0	0	0	0
Ocetis unicolor	*p*	0	0	0	0	0
Zellolisica cheira	*cb*	0	0	0	0	0
Scirtidae	*cb*	1	0	11	0	0
Huxelhydrus syntheticus	*p*	0	0	0	0	0
Antiporus stigosulus	*p*	0	0	1	0	0
Liodessus deflectus	*p*	0	0	0	0	0
Hydrophilidae	*p*	0	0	0	0	0
Antiporus femoralis	p	0	0	0	0	0
Ptilodactylidae	*cb*	0	0	0	0	0
Hydraenidae	*sh*	0	0	0	0	0
Elmidae	*cb*	0	0	0	1	5
Hexatomini sp.	*cb*	0	0	1	0	0
Psychodidae	*cb*	0	0	0	0	0
Ceratopogonidae	*p*	0	0	0	0	0
Sciomyzidae	*p*	0	0	0	0	0
Limonia sp.	*sh*	5	0	3	0	0
Muscidae	*cb*	3	0	1	0	0
Aphrophila sp.	*cb*	0	0	0	0	1
Zelandotipula sp.	*cb*	0	0	1	0	0
Tabanidae	*p*	0	0	0	0	0
Eriopterini	*cb*	0	3	0	1	1
N*eocurupira*	*sc*	0	0	0	0	0
Stradiomyidae	*cb*	0	0	0	0	0
Empididae	*cb*	0	0	0	0	0
culex	*f*	0	0	0	0	0
Nothodixa	*cb*	0	0	0	0	0
Austrosimulium	*f*	10	0	0	3	3
Tanypodinae	*p*	1	1	3	0	1
Chironominae	*cb*	0	0	0	0	0
Diamesinae	*cb*	20	0	3	1	0
Orthocladiinae	*cb*	20	10	5	3	3
Potamopyrgus antipodarum	*sc*	0	0	0	0	0
Sphaeriadae	*f*	0	0	0	0	0
Lymnae tomentosa	*sc*	0	0	0	0	0
Phreatogammerus sp.	*cb*	0	0	0	0	0
Paraleptamphopus sp.	*cb*	20	0	0	0	0
Ostracod	*f*	0	0	0	0	0
Turbellaria	*p*	1	3	3	0	0

Prorhynchus putealis	*p*	0	0	1	0	0
Hirudinae	*p*	0	0	0	0	0
Acari	*p*	0	0	0	0	0
Oniscoidea	*cb*	0	0	0	0	0
Oligochaeta	*cb*	0	3	3	3	0
Nematomorpha		0	0	0	0	0
Archicauliodes diversus	*p*	0	0	0	0	0
Sigara sp.	hp	0	0	1	0	0

Taxa	***ffg***	**Klondyke 19**	**Klondyke 20**	**Klondyke 21**	**Klondyke 22**	**Klondyke hill**
Nannochorista philpotti	*p*	0	0	0	0	0
Kempynus sp.	*p*	1	0	0	0	0
Coloburiscus humeralis	*f*	0	0	0	0	0
Nesameletus ornatus	*cb*	0	0	0	0	0
Nesameletus austrinus	*cb*	0	0	0	0	10
Oniscigaster wakefieldi	*cb*	0	0	0	0	0
Austroclima sp.	*cb*	0	0	0	0	0
Deleatidium spp.	*cb*	5	1	20	11	10
Austroperla cyrene	*sh*	0	0	0	0	3
Stenaperla maclellani	*p*	0	0	1	0	10
Taraperla howsei	*cb*	0	0	0	0	0
Zelandoperla sp.	*cb*	1	0	0	0	1
Zelandobius unicolor	*cb*	0	0	0	0	1
Zelandobius pilosus	*cb*	0	0	0	0	0
Zelandobius confusus	*cb*	0	0	0	0	1
Zelandobius furcillatus	*cb*	0	0	0	0	1
Cristaperla sp.	*cb*	0	0	0	0	0
Spaniocerca sp.	*cb*	0	0	0	0	3
Megaleptoperla grandis	*p*	0	0	0	0	0
Halticoperla viridans	*cb*	0	0	0	0	1
Aoteapsyche colonica	*f*	0	0	0	0	0
Beraeoptera roria	*cb*	0	0	0	0	0
Oxyethira sp.	*hp*	1	1	11	3	0
Paroxyethira eatoni	*hp*	0	0	0	0	0
Psilochorema sp.	*p*	0	0	3	0	0
Olinga feredayi	*cb*	0	0	0	0	0
Hydrobiosidae indent.	*p*	0	0	0	0	0
Hydrobiosis charadraea	*p*	0	0	0	0	0
Hydrobiosis clavigera	*p*	0	0	0	0	0
Hydrobiosis parumbripennis	*p*	0	1	1	1	0
Hydrobiosis torrentis	*p*	0	0	0	0	0
Hydrobiosis soro	*p*	0	0	0	0	0
Hydrobiosis neadelphus (styx)	*p*	0	0	0	0	0
Hydrobiosis silvicola-gp	*p*	0	0	0	0	0
Hydrobiosis chalcodes	*p*	0	0	0	0	0
Hydrobiosis harpidiosa	*p*	0	0	0	0	0
Costachorema xanthopterum	*p*	0	0	0	0	0
Polyplectropus sp.	*p*	0	0	0	0	0
Philorheithrus agilis	*p*	0	0	0	0	0

Oeconesus sp.	*cb*	0	0	0	0	0
Hudsonema amabile	*p*	0	0	0	0	0
Hudsonema alienium	*p*	0	0	0	0	0
Triplectides obsoletus	*sh*	0	0	0	0	0
Pycnocentrodes sp.	*cb*	1	1	5	1	0
Pycnocentria funerea	*cb*	0	0	0	0	0
Pycnocentria evecta	*cb*	0	0	3	0	0
Edpercivalia sp.	*p*	0	0	0	0	0
Hydrobiosella sp.	*f*	0	0	0	0	1
Hydrochorema tenuicaudatum	*p*	0	0	0	0	0
T*railochorema*	p	0	0	0	0	0
Costachorema psaropterum	*p*	0	0	0	0	1
Pycnocentria sylvestris	*cb*	0	0	0	0	0
Zealandopsyche ingens	*sh*	0	0	0	0	3
Ocetis unicolor	*p*	0	0	0	0	1
Zellolisica cheira	*cb*	0	3	0	0	0
Scirtidae	*cb*	20	3	0	13	0
Huxelhydrus syntheticus	*p*	0	0	0	0	0
Antiporus stigosulus	*p*	0	0	0	0	0
Liodessus deflectus	*p*	0	1	0	0	0
Hydrophilidae	*p*	0	0	0	0	0
Antiporus femoralis	p	0	0	0	0	0
Ptilodactylidae	*cb*	0	0	0	0	0
Hydraenidae	*sh*	0	0	0	0	1
Elmidae	*cb*	0	0	0	0	1
Hexatomini sp.	*cb*	0	0	1	0	1
Psychodidae	*cb*	0	0	0	0	0
Ceratopogonidae	*p*	0	0	0	0	1
Sciomyzidae	*p*	0	0	0	0	0
Limonia sp.	*sh*	1	13	3	5	0
Muscidae	*cb*	1	1	1	3	0
Aphrophila sp.	*cb*	0	0	3	0	0
Zelandotipula sp.	*cb*	1	0	0	0	0
Tabanidae	*p*	0	0	0	0	0
Eriopterini	*cb*	0	0	0	0	0
Neocurupira	*sc*	0	0	0	0	0
Stradiomyidae	*cb*	0	0	0	0	0
Empididae	*cb*	0	0	0	0	0
culex	*f*	0	0	0	0	0
Nothodixa	*cb*	0	0	0	0	0
Austrosimulium	*f*	0	3	3	50	3
Tanypodinae	*p*	0	0	0	0	10
Chironominae	*cb*	0	0	0	0	0
Diamesinae	*cb*	3	3	13	13	0
Orthocladiinae	*cb*	100	11	0	11	10
Potamopyrgus antipodarum	*sc*	1	0	0	0	3
Sphaeriadae	*f*	0	0	0	0	0
Lymnae tomentosa	*sc*	0	0	0	0	0
Phreatogammerus sp.	*cb*	0	0	0	0	0
Paraleptamphopus sp.	*cb*	0	0	13	20	0

Ostracod	*f*	0	0	10	0	0
Turbellaria	*p*	0	0	1	0	3
Prorhynchus putealis	*p*	0	1	0	0	0
Hirudinae	*p*	0	0	0	1	0
Acari	*p*	0	0	0	0	1
Oniscoidea	*cb*	0	0	0	0	0
Oligochaet	*cb*	0	0	1	0	1
Nematomorpha		0	0	0	0	0
Archicauliodes diversus	*p*	0	0	0	0	0
Sigara sp.	hp	0	0	0	0	0

Taxa	***ffg***	**Cora Lyn 23**	**Cora Lyn 24**	**Cora Lyn 25**	**Cora Lyn 26**	**Cora Lyn 27**
Nannochorista philpotti	*p*	0	0	0	0	0
Kempynus sp.	*p*	0	0	0	0	0
Coloburiscus humeralis	*f*	0	0	0	0	0
Nesameletus ornatus	*cb*	3	0	0	0	1
Nesameletus austrinus	*cb*	0	0	0	0	0
Oniscigaster wakefieldi	*cb*	0	0	0	0	0
Austroclima sp.	*cb*	0	0	0	0	0
Deleatidium spp.	*cb*	13	5	20	5	60
Austroperla cyrene	*sh*	0	0	0	0	0
Stenaperla maclellani	*p*	0	0	0	0	0
Taraperla howsei	*cb*	0	0	0	0	0
Zelandoperla sp.	*cb*	0	0	0	0	3
Zelandobius unicolor	*cb*	0	0	0	0	0
Zelandobius pilosus	*cb*	0	0	0	0	0
Zelandobius confusus	*cb*	0	0	0	0	0
Zelandobius furcillatus	*cb*	1	1	0	0	3
Cristaperla sp.	*cb*	0	0	0	0	0
Spaniocerca sp.	*cb*	0	0	0	0	0
Megaleptoperla grandis	*p*	0	0	0	0	0
Halticoperla viridans	*cb*	0	0	0	0	0
Aoteapsyche colonica	*f*	0	0	0	0	0
Beraeoptera roria	*cb*	0	0	0	0	0
Oxyethira sp.	*hp*	3	11	5	1	0
Paroxyethira eatoni	*hp*	0	0	0	0	0
Psilochorema sp.	*p*	1	1	1	1	1
Olinga feredayi	*cb*	0	0	0	0	0
Hydrobiosidae indent.	*p*	1	1	0	0	1
Hydrobiosis charadraea	*p*	0	0	0	0	0
Hydrobiosis clavigera	*p*	1	0	0	3	0
Hydrobiosis parumbripennis	*p*	13	1	3	3	3
Hydrobiosis torrentis	*p*	0	0	0	0	0
Hydrobiosis soro	*p*	0	0	0	0	0
Hydrobiosis neadelphus (styx)	*p*	0	0	0	0	0
Hydrobiosis silvicola-gp	*p*	0	0	0	0	0
Hydrobiosis chalcodes	*p*	3	0	0	0	0
Hydrobiosis harpidiosa	*p*	0	0	0	0	1
Costachorema xanthopterum	*p*	0	0	0	0	0

Polyplectropus sp.	*p*	0	0	0	0	0
Philorheithrus agilis	*p*	0	0	0	0	0
Oeconesus sp.	*cb*	0	1	1	0	0
Hudsonema amabile	*p*	0	1	1	0	0
Hudsonema alienium	*p*	0	0	0	0	0
Triplectides obsoletus	*sh*	0	0	0	0	0
Pycnocentrodes sp.	*cb*	5	13	1	5	0
Pycnocentria funerea	*cb*	1	0	0	0	0
Pycnocentria evecta	*cb*	1	1	5	0	0
Edpercivalia sp.	*p*	0	0	0	0	0
Hydrobiosella sp.	*f*	0	0	0	0	0
Hydrochorema tenuicaudatum	*p*	0	0	0	0	0
Trailochorema	p	0	0	0	1	0
Costachorema psaropterum	*p*	0	0	0	0	0
Pycnocentria sylvestris	*cb*	0	0	0	0	0
Zealandopsyche ingens	*sh*	0	0	0	0	0
Ocetis unicolor	*p*	0	0	0	0	0
Zellolisica cheira	*cb*	0	0	0	0	0
Scirtidae	*cb*	0	0	0	0	0
Huxelhydrus syntheticus	*p*	0	0	0	0	0
Antiporus stigosulus	*p*	0	0	0	3	0
Liodessus deflectus	*p*	0	1	0	0	0
Hydrophilidae	*p*	0	0	0	0	0
Antiporus femoralis	p	0	0	0	0	0
Ptilodactylidae	*cb*	0	0	0	0	0
Hydraenidae	*sh*	0	0	0	0	0
Elmidae	*cb*	5	0	1	5	1
Hexatomini sp.	*cb*	1	0	0	0	0
Psychodidae.	*cb*	0	0	0	0	0
Ceratopogonidae	*p*	0	0	0	0	0
Sciomyzidae	*p*	0	0	0	0	0
Limonia sp.	*sh*	1	11	1	5	0
Muscidae	*cb*	1	1	5	5	0
Aphrophila sp.	*cb*	0	0	1	3	0
Zelandotipula sp.	*cb*	0	0	0	0	0
Tabanidae	*p*	0	0	0	0	0
Eriopterini	*cb*	1	0	0	0	1
Neocurupira	*sc*	0	0	0	0	0
Stradiomyidae	*cb*	1	0	0	0	0
Empididae	*cb*	0	0	0	0	0
culex	*f*	0	0	0	0	0
Nothodixa	*cb*	0	0	0	0	0
Austrosimulium	*f*	0	0	1	1	1
Tanypodinae	*p*	3	20	1	0	0
Chironominae	*cb*	0	0	0	0	0
Diamesinae	*cb*	13	3	10	5	0
Orthocladiinae	*cb*	5	13	100	1	3
Potamopyrgus antipodarum	*sc*	0	51	1	0	0
Sphaeriadae	*f*	0	0	0	0	0
Lymnae tomentosa	*sc*	0	5	0	0	0

Phreatogammerus sp.	*cb*	0	0	0	3	0
Paraleptamphopus sp.	*cb*	1	3	0	5	0
Ostracod	*f*	0	0	0	0	0
Turbellaria	*p*	1	0	0	0	0
Prorhynchus putealis	*p*	0	0	1	0	0
Hirudinae	*p*	0	0	0	0	0
Acari	*p*	0	0	0	0	0
Oniscoidea	*cb*	0	0	0	0	0
Oligochaeta	*cb*	0	0	0	0	0
Nematomorpha		0	0	0	0	0
Archicauliodes diversus	*p*	0	0	0	0	0
Sigara sp.	hp	0	0	0	0	0

Taxa	***ffg***	**Cora Lyn 28**	**Cora Lyn 29**	**Cora Lyn hill**	**One Tree Swamp 30**	**One Tree Swamp 31**
Nannochorista philpotti	*p*	0	0	0	0	0
Kempynus sp.	*p*	0	0	0	0	0
Coloburiscus humeralis	*f*	0	0	0	0	0
Nesameletus ornatus	*cb*	0	0	0	0	1
Nesameletus austrinus	*cb*	0	0	0	0	0
Oniscigaster wakefieldi	*cb*	0	0	0	0	0
Austroclima sp.	*cb*	0	0	3	0	0
Deleatidium spp.	*cb*	100	0	10	20	20
Austroperla cyrene	*sh*	0	0	0	1	3
Stenaperla maclellani	*p*	0	0	3	0	0
Taraperla howsei	*cb*	0	0	0	0	0
Zelandoperla sp.	*cb*	1	0	3	0	0
Zelandobius unicolor	*cb*	0	1	0	0	0
Zelandobius pilosus	*cb*	0	1	0	0	5
Zelandobius confusus	*cb*	0	0	1	0	0
Zelandobius furcillatus	*cb*	0	3	0	0	0
Cristaperla sp.	*cb*	0	0	0	0	0
Spaniocerca sp.	*cb*	1	0	0	0	0
Megaleptoperla grandis	*p*	0	0	0	0	0
Halticoperla viridans	*cb*	0	0	0	0	0
Aoteapsyche colonica	*f*	0	0	10	0	0
Beraeoptera roria	*cb*	0	0	0	0	0
Oxyethira sp.	*hp*	3	3	0	0	1
Paroxyethira eatoni	*hp*	1	0	0	0	0
Psilochorema sp.	*p*	3	3	0	1	3
Olinga feredayi	*cb*	0	0	1	0	0
Hydrobiosidae indent.	*p*	1	1	1	0	0
Hydrobiosis charadraea	*p*	0	0	0	0	0
Hydrobiosis clavigera	*p*	3	0	0	0	0
Hydrobiosis parumbripennis	*p*	3	3	0	3	1
Hydrobiosis torrentis	*p*	0	0	0	0	0
Hydrobiosis soro	*p*	0	0	0	0	0
Hydrobiosis neadelphus (styx)	*p*	0	0	0	0	0
Hydrobiosis silvicola-gp	*p*	0	0	0	0	0
Hydrobiosis chalcodes	*p*	0	0	0	0	0
Hydrobiosis harpidiosa	*p*	0	0	0	0	0

Costachorema xanthopterum	*p*	0	0	0	0	0
Polyplectropus sp.	*p*	1	5	0	0	0
Philorheithrus agilis	*p*	0	0	0	0	0
Oeconesus sp.	*cb*	0	3	3	1	0
Hudsonema amabile	*p*	1	11	0	1	1
Hudsonema alienium	*p*	0	1	0	0	1
Triplectides obsoletus	*sh*	0	0	0	0	0
Pycnocentrodes sp.	*cb*	260	20	1	13	5
Pycnocentria funerea	*cb*	50	0	0	0	0
Pycnocentria evecta	*cb*	50	11	0	13	5
Edpercivalia sp.	*p*	0	0	0	0	0
Hydrobiosella sp.	*f*	0	0	3	0	0
Hydrochorema tenuicaudatum	*p*	0	0	0	0	0
Trailochorema	p	0	0	0	0	0
Costachorema psaropterum	*p*	0	0	0	0	0
Pycnocentria sylvestris	*cb*	0	0	1	0	0
Zealandopsyche ingens	*sh*	0	0	0	0	0
Ocetis unicolor	*p*	0	0	0	0	0
Zellolisica cheira	*cb*	0	0	0	0	0
Scirtidae	*cb*	0	0	10	0	0
Huxelhydrus syntheticus	*p*	0	0	0	0	0
Antiporus stigosulus	*p*	0	0	0	0	0
Liodessus deflectus	*p*	0	0	0	1	0
Hydrophilidae	*p*	0	0	1	0	0
Antiporus femoralis	p	0	0	0	0	0
Ptilodactylidae	*cb*	0	0	0	0	0
Hydraenidae	*sh*	0	0	0	0	0
Elmidae	*cb*	3	0	10	0	0
Hexatomini sp.	*cb*	1	1	1	0	0
Psychodidae	*cb*	0	0	0	0	0
Ceratopogonidae	*p*	0	0	0	0	0
Sciomyzidae	*p*	0	0	0	0	0
Limonia sp.	*sh*	1	0	0	1	0
Muscidae	*cb*	3	1	1	1	0
Aphrophila sp.	*cb*	3	0	0	0	0
Zelandotipula sp.	*cb*	0	0	0	0	0
Tabanidae	*p*	0	0	0	0	0
Eriopterini	*cb*	1	0	0	1	0
Neocurupira	*sc*	0	0	0	0	0
Stradiomyidae	*cb*	1	0	0	0	0
Empididae	*cb*	0	0	0	0	0
c*ulex*	*f*	0	0	0	0	0
Nothodixa	*cb*	0	0	0	0	0
Austrosimulium	*f*	1	3	3	0	0
Tanypodinae	*p*	3	13	0	1	1
Chironominae	*cb*	0	0	0	1	0
Diamesinae	*cb*	11	0	10	3	1
Orthocladiinae	*cb*	53	13	10	5	3
Potamopyrgus antipodarum	*sc*	20	20	50	60	5
Sphaeriadae	*f*	0	11	0	0	1
Lymnae tomentosa	*sc*	0	0	0	0	0
Phreatogammerus sp.	*cb*	0	0	0	0	1

Paraleptamphopus sp.	*cb*	5	0	0	1	1
Ostracod	*f*	0	3	0	3	10
Turbellaria	*p*	5	0	0	11	10
Prorhynchus putealis	*p*	0	0	0	1	3
Hirudinae	*p*	0	0	0	0	0
Acari	*p*	0	0	0	0	1
Oniscoidea	*cb*	0	0	0	0	0
Oligochaeta	*cb*	3	0	3	3	0
Nematomorpha		0	0	0	0	0
Archicauliodes diversus	*p*	0	0	0	0	0
Sigara sp.	hp	0	0	0	0	0

Taxa	***ffg***	**One Tree Swamp 32**	**One Tree Swamp 33**	**One Tree Swamp 34**	**One Tree Swamp 35**	**One Tree Swamp 36**
Nannochorista philpotti	*p*	0	0	0	0	0
Kempynus sp.	*p*	0	0	0	0	0
Coloburiscus humeralis	*f*	0	0	0	0	0
Nesameletus ornatus	*cb*	0	1	20	0	0
Nesameletus austrinus	*cb*	0	0	0	0	0
Oniscigaster wakefieldi	*cb*	0	0	0	0	0
Austroclima sp.	*cb*	0	0	0	0	0
Deleatidium spp.	*cb*	20	20	60	20	1
Austroperla cyrene	*sh*	0	0	0	1	0
Stenaperla maclellani	*p*	0	0	0	0	0
Taraperla howsei	*cb*	0	0	0	0	0
Zelandoperla sp.	*cb*	0	5	1	0	0
Zelandobius unicolor	*cb*	0	1	0	0	0
Zelandobius pilosus	*cb*	3	0	0	1	0
Zelandobius confusus	*cb*	0	0	0	0	0
Zelandobius furcillatus	*cb*	0	3	5	0	0
Cristaperla sp.	*cb*	0	0	0	0	0
Spaniocerca sp.	*cb*	0	0	0	0	0
Megaleptoperla grandis	*p*	0	0	0	0	0
Halticoperla viridans	*cb*	0	0	0	0	0
Aoteapsyche colonica	*f*	0	0	0	0	0
Beraeoptera roria	*cb*	0	0	0	0	0
Oxyethira sp.	*hp*	0	0	1	1	5
Paroxyethira eatoni	*hp*	0	0	0	0	0
Psilochorema sp.	*p*	1	1	1	1	3
Olinga feredayi	*cb*	0	0	0	0	0
Hydrobiosidae indent.	*p*	0	1	1	1	1
Hydrobiosis charadraea	*p*	0	0	0	0	0
Hydrobiosis clavigera	*p*	0	0	1	0	0
Hydrobiosis parumbripennis	*p*	1	0	3	0	0
Hydrobiosis torrentis	*p*	0	0	0	0	0
Hydrobiosis soro	*p*	0	0	1	0	0
Hydrobiosis neadelphus (styx)	*p*	0	0	0	0	0
Hydrobiosis silvicola-gp	*p*	0	0	0	0	0

Hydrobiosis chalcodes	*p*	0	0	1	0	0
Hydrobiosis harpidiosa	*p*	0	1	0	0	0
Costachorema xanthopterum	*p*	0	0	0	0	0
Polyplectropus sp.	*p*	0	0	1	0	0
Philorheithrus agilis	*p*	0	0	0	0	0
Oeconesus sp.	*cb*	1	0	0	1	11
Hudsonema amabile	*p*	1	0	0	0	0
Hudsonema alienium	*p*	3	0	1	1	0
Triplectides obsoletus	*sh*	0	0	0	0	0
Pycnocentrodes sp.	*cb*	20	1	5	5	5
Pycnocentria funerea	*cb*	3	0	0	0	0
Pycnocentria evecta	*cb*	13	0	1	20	0
Edpercivalia sp.	*p*	0	0	0	0	0
Hydrobiosella sp.	*f*	0	0	0	0	0
Hydrochorema tenuicaudatum	*p*	0	0	0	0	0
Trailochorema	p	0	0	0	0	0
Costachorema psaropterum	*p*	0	1	0	0	0
Pycnocentria sylvestris	*cb*	0	0	0	0	0
Zealandopsyche ingens	*sh*	0	0	0	0	0
Ocetis unicolor	*p*	0	0	0	0	0
Zellolisica cheira	*cb*	0	0	0	0	0
Scirtidae	*cb*	3	50	0	5	0
Huxelhydrus syntheticus	*p*	0	0	0	0	0
Antiporus stigosulus	*p*	0	0	0	0	0
Liodessus deflectus	*p*	0	0	0	0	0
Hydrophilidae	*p*	0	0	0	0	0
Antiporus femoralis	p	0	0	0	0	0
Ptilodactylidae	*cb*	0	0	0	0	0
Hydraenidae	*sh*	0	0	0	0	0
Elmidae	*cb*	0	1	5	0	0
Hexatomini sp.	*cb*	0	0	1	0	1
Psychodidae.	*cb*	0	0	0	0	0
Ceratopogonidae	*p*	0	0	0	0	1
Sciomyzidae	*p*	0	0	0	0	0
Limonia sp.	*sh*	1	0	0	1	0
Muscidae	*cb*	1	0	0	1	1
Aphrophila sp.	*cb*	0	0	0	1	0
Zelandotipula sp.	*cb*	0	0	0	0	0
Tabanidae	*p*	0	0	0	0	0
Eriopterini	*cb*	0	1	1	0	1
N*eocurupira*	*sc*	0	0	0	0	0
Stradiomyidae	*cb*	0	0	0	0	0
Empididae	*cb*	0	0	0	0	0
culex	*f*	0	0	0	0	0
Nothodixa	*cb*	0	0	0	0	0
Austrosimulium	*f*	0	0	1	3	0
Tanypodinae	*p*	1	0	1	0	13
Chironominae	*cb*	0	0	0	0	0
Diamesinae	*cb*	20	0	0	3	0

Orthocladiinae	*cb*	13	5	1	20	13
Potamopyrgus antipodarum	*sc*	13	0	1	20	60
Sphaeriadae	*f*	3	0	0	0	0
Lymnae tomentosa	*sc*	0	0	0	0	0
Phreatogammerus sp.	*cb*	0	0	0	0	0
Paraleptamphopus sp.	*cb*	1	0	5	0	11
Ostracod	*f*	3	0	0	0	20
Turbellaria	*p*	10	0	0	1	3
Prorhynchus putealis	*p*	0	0	0	0	0
Hirudinae	*p*	0	0	0	0	0
Acari	*p*	0	0	0	0	0
Oniscoidea	*cb*	0	0	0	0	0
Oligochaeta	*cb*	3	0	0	3	0
Nematomorpha		0	0	0	0	0
Archicauliodes diversus	*p*	0	0	0	0	0
Sigara sp.	hp	0	0	0	0	0

Taxa	***ffg***	**One Tree Swamp hill**	**Waimak Spring 37**	**Waimak Spring 38**	**Waimak Spring 39**	**Waimak Spring 40**
Nannochorista philpotti	*p*	0	0	0	0	0
Kempynus sp.	*p*	0	0	0	0	0
Coloburiscus humeralis	*f*	0	0	0	1	0
Nesameletus ornatus	*cb*	0	0	1	3	1
Nesameletus austrinus	*cb*	3	0	0	0	0
Oniscigaster wakefieldi	*cb*	0	0	0	0	0
Austroclima sp.	*cb*	0	0	0	0	0
Deleatidium spp.	*cb*	10	5	3	60	53
Austroperla cyrene	*sh*	3	1	0	0	0
Stenaperla maclellani	*p*	0	0	0	0	0
Taraperla howsei	*cb*	3	0	0	0	0
Zelandoperla sp.	*cb*	1	0	0	0	5
Zelandobius unicolor	*cb*	0	0	0	3	3
Zelandobius pilosus	*cb*	0	0	1	1	1
Zelandobius confusus	*cb*	1	0	0	0	0
Zelandobius furcillatus	*cb*	1	0	0	10	3
Cristaperla sp.	*cb*	0	0	0	0	0
Spaniocerca sp.	*cb*	0	0	0	0	0
Megaleptoperla grandis	*p*	0	0	0	0	0
Halticoperla viridans	*cb*	0	0	0	0	0
Aoteapsyche colonica	*f*	0	0	0	5	0
Beraeoptera roria	*cb*	0	0	0	0	1
Oxyethira sp.	*hp*	0	0	11	3	0
Paroxyethira eatoni	*hp*	0	0	1	1	0
Psilochorema sp.	*p*	0	5	3	3	1
Olinga feredayi	*cb*	1	0	0	1	0
Hydrobiosidae indent.	*p*	0	0	1	1	1

Hydrobiosis charadraea	*p*	0	0	0	0	0
Hydrobiosis clavigera	*p*	0	0	0	0	0
Hydrobiosis parumbripennis	*p*	0	1	1	5	0
Hydrobiosis torrentis	*p*	0	0	0	0	0
Hydrobiosis soro	*p*	0	0	0	1	0
Hydrobiosis neadelphus (styx)	*p*	0	0	0	0	0
Hydrobiosis silvicola-gp	*p*	0	0	0	0	0
Hydrobiosis chalcodes	*p*	0	0	0	0	0
Hydrobiosis harpidiosa	*p*	0	0	0	0	0
Costachorema xanthopterum	*p*	0	0	0	0	0
Polyplectropus sp.	*p*	0	1	3	0	0
Philorheithrus agilis	*p*	0	0	0	0	0
Oeconesus sp.	*cb*	1	1	3	0	0
Hudsonema amabile	*p*	0	0	0	1	0
Hudsonema alienium	*p*	0	0	0	0	0
Triplectides obsoletus	*sh*	0	0	0	0	0
Pycnocentrodes sp.	*cb*	0	1	13	13	1
Pycnocentria funerea	*cb*	0	0	1	0	0
Pycnocentria evecta	*cb*	0	5	0	13	1
Edpercivalia sp.	*p*	0	0	0	0	0
Hydrobiosella sp.	*f*	0	0	0	0	0
Hydrochorema tenuicaudatum	*p*	0	0	0	0	0
Trailochorema	p	0	0	0	0	0
Costachorema psaropterum	*p*	0	0	0	0	0
Pycnocentria sylvestris	*cb*	1	0	0	0	0
Zealandopsyche ingens	*sh*	3	0	0	0	0
Ocetis unicolor	*p*	0	0	0	0	0
Zellolisica cheira	*cb*	0	0	0	0	0
Scirtidae	*cb*	1	0	0	0	0
Huxelhydrus syntheticus	*p*	0	0	0	0	0
Antiporus stigosulus	*p*	0	0	0	0	0
Liodessus deflectus	*p*	0	0	0	0	0
Hydrophilidae	*p*	0	0	0	0	0
Antiporus femoralis	p	1	0	0	0	0
Ptilodactylidae	*cb*	0	0	0	0	0
Hydraenidae	*sh*	1	0	0	0	0
Elmidae	*cb*	3	0	0	1	3
Hexatomini sp.	*cb*	0	0	0	0	0
Psychodidae	*cb*	0	0	0	0	0
Ceratopogonidae	*p*	0	0	0	0	0
Sciomyzidae	*p*	0	0	0	0	0
Limonia sp.	*sh*	0	1	1	0	0
Muscidae	*cb*	1	1	3	1	0
Aphrophila sp.	*cb*	0	0	0	1	0
Zelandotipula sp.	*cb*	0	1	0	0	0
Tabanidae	*p*	0	0	0	0	0
Eriopterini	*cb*	0	0	0	1	1
Neocurupira	*sc*	0	0	0	0	0
Stradiomyidae	*cb*	0	0	1	0	0
Empididae	*cb*	0	0	0	0	0
culex	*f*	0	0	0	0	0
Nothodixa	*cb*	0	0	0	0	0
Austrosimulium	*f*	0	0	0	3	3
Tanypodinae	*p*	0	5	53	3	1

Chironominae	*cb*	0	0	50	0	0
Diamesinae	*cb*	0	0	0	20	1
Orthocladiinae	*cb*	3	5	250	20	5
Potamopyrgus antipodarum	*sc*	10	1	13	50	0
Sphaeriadae	*f*	0	0	0	0	0
Lymnae tomentosa	*sc*	0	1	3	1	0
Phreatogammerus sp.	*cb*	0	0	0	0	0
Paraleptamphopus sp.	*cb*	0	1	1	0	0
Ostracod	*f*	0	5	0	10	0
Turbellaria	*p*	1	1	0	5	0
Prorhynchus putealis	*p*	0	0	0	0	0
Hirudinae	*p*	0	0	0	0	0
Acari	*p*	0	0	0	0	0
Oniscoidea	*cb*	0	0	0	0	0
Oligochaeta	*cb*	0	0	3	1	0
Nematomorpha		0	0	0	0	0
Archicauliodes diversus	*p*	0	0	0	0	0
Sigara sp.	hp	0	0	0	0	0

Taxa	***ffg***	**Waimak Spring 41**	**Waimak Spring 42**	**Waimak Spring hill**	**Hawdon 43**	**Hawdon 44**
Nannochorista philpotti	*p*	0	0	0	1	0
Kempynus sp.	*p*	0	0	0	0	0
Coloburiscus humeralis	*f*	1	1	3	0	0
Nesameletus ornatus	*cb*	0	3	0	0	0
Nesameletus austrinus	*cb*	0	0	0	0	0
Oniscigaster wakefieldi	*cb*	0	0	3	0	0
Austroclima sp.	*cb*	0	0	0	0	0
Deleatidium spp.	*cb*	20	60	50	1	1
Austroperla cyrene	*sh*	0	1	0	3	0
Stenaperla maclellani	*p*	0	0	0	1	1
Taraperla howsei	*cb*	0	0	0	1	0
Zelandoperla sp.	*cb*	0	1	3	0	0
Zelandobius unicolor	*cb*	0	0	1	3	0
Zelandobius pilosus	*cb*	0	0	0	1	5
Zelandobius confusus	*cb*	0	0	0	0	0
Zelandobius furcillatus	*cb*	0	0	0	0	0
Cristaperla sp.	*cb*	0	0	0	3	0
Spaniocerca sp.	*cb*	0	0	0	3	20
Megaleptoperla grandis	*p*	0	0	0	0	0
Halticoperla viridans	*cb*	0	0	0	1	0
Aoteapsyche colonica	*f*	5	1	3	0	0
Beraeoptera roria	*cb*	0	1	3	0	0
Oxyethira sp.	*hp*	3	3	0	1	1
Paroxyethira eatoni	*hp*	0	0	0	0	0
Psilochorema sp.	*p*	1	3	1	3	1
Olinga feredayi	*cb*	5	1	3	0	0
Hydrobiosidae indent.	*p*	5	1	1	1	1
Hydrobiosis charadraea	*p*	0	0	0	0	0

Hydrobiosis clavigera	*p*	0	0	0	0	0
Hydrobiosis parumbripennis	*p*	1	1	0	3	5
Hydrobiosis torrentis	*p*	0	0	0	0	0
Hydrobiosis soro	*p*	0	1	0	0	0
Hydrobiosis neadelphus (styx)	*p*	0	0	0	0	0
Hydrobiosis silvicola-gp	*p*	0	0	0	0	0
Hydrobiosis chalcodes	*p*	0	0	0	0	1
Hydrobiosis harpidiosa	*p*	0	0	0	0	0
Costachorema xanthopterum	*p*	0	1	0	0	0
Polyplectropus sp.	*p*	0	1	0	0	0
Philorheithrus agilis	*p*	0	1	0	0	1
Oeconesus sp.	*cb*	0	3	0	1	1
Hudsonema amabile	*p*	3	0	0	0	0
Hudsonema alienium	*p*	3	1	0	0	1
Triplectides obsoletus	*sh*	0	0	0	3	0
Pycnocentrodes sp.	*cb*	5	13	1	1	3
Pycnocentria funerea	*cb*	0	0	0	1	0
Pycnocentria evecta	*cb*	1	60	0	0	0
Edpercivalia sp.	*p*	0	0	0	0	0
Hydrobiosella sp.	*f*	0	0	1	0	0
Hydrochorema tenuicaudatum	*p*	0	0	0	0	0
Trailochorema	p	0	0	0	0	0
Costachorema psaropterum	*p*	0	0	0	0	0
Pycnocentria sylvestris	*cb*	0	0	0	0	0
Zealandopsyche ingens	*sh*	0	0	0	1	0
Ocetis unicolor	*p*	0	0	0	0	0
Zellolisica cheira	*cb*	0	0	0	1	0
Scirtidae	*cb*	0	1	0	1	1
Huxelhydrus syntheticus	*p*	0	0	0	0	0
Antiporus stigosulus	*p*	0	0	0	0	0
Liodessus deflectus	*p*	0	0	0	0	0
Hydrophilidae	*p*	0	0	0	0	0
Antiporus femoralis	p	0	0	0	0	0
Ptilodactylidae	*cb*	0	0	0	0	0
Hydraenidae	*sh*	0	0	0	0	0
Elmidae	*cb*	5	0	3	0	0
Hexatomini sp.	*cb*	0	0	1	0	0
Psychodidae	*cb*	0	0	0	0	0
Ceratopogonidae	*p*	0	1	0	0	0
Sciomyzidae.	*p*	0	0	0	0	0
Limonia sp.	*sh*	0	0	0	3	1
Muscidae	*cb*	0	3	0	0	5
Aphrophila sp.	*cb*	1	0	3	0	0
Zelandotipula sp.	*cb*	0	0	0	0	0
Tabanidae	*p*	1	0	0	0	0
Eriopterini	*cb*	0	0	3	0	0
Neocurupira	*sc*	0	0	0	0	0
Stradiomyidae	*cb*	0	0	0	0	0
Empididae	*cb*	0	0	0	0	0
culex	*f*	0	0	0	0	0
Nothodixa	*cb*	0	0	0	0	0
Austrosimulium	*f*	5	1	10	0	3
Tanypodinae	*p*	5	3	1	3	0
Chironominae	*cb*	0	0	1	53	0

Diamesinae	*cb*	1	10	0	10	10
Orthocladiinae	*cb*	50	51	10	50	20
Potamopyrgus antipodarum	*sc*	20	53	0	20	20
Sphaeriadae	*f*	0	1	0	0	0
Lymnae tomentosa	*sc*	0	0	0	0	0
Phreatogammerus sp.	*cb*	0	0	0	0	0
Paraleptamphopus sp.	*cb*	0	0	0	53	20
Ostracod	*f*	0	0	0	1	0
Turbellaria	*p*	0	3	0	5	1
Prorhynchus putealis	*p*	0	0	0	0	1
Hirudinae	*p*	0	0	0	0	0
Acari	*p*	0	0	0	0	0
Oniscoidea	*cb*	0	0	0	0	0
Oligochaeta	*cb*	0	0	1	0	0
Nematomorpha		0	0	0	0	0
Archicauliodes diversus	*p*	0	0	3	0	0
Sigara sp.	hp	0	0	0	0	0

Taxa	***ffg***	**Hawdon 45**	**Hawdon 46**	**Hawdon 47**	**Hawdon 48**	**Hawdon 49**	**Hawdon hill**
Nannochorista philpotti	*p*	0	0	0	0	0	0
Kempynus sp.	*p*	0	0	0	0	0	0
Coloburiscus humeralis	*f*	0	0	0	0	0	0
Nesameletus ornatus	*cb*	0	0	0	1	0	0
Nesameletus austrinus	*cb*	0	0	0	0	0	0
Oniscigaster wakefieldi	*cb*	0	0	0	0	0	0
Austroclima sp.	*cb*	0	0	0	0	0	0
Deleatidium spp.	*cb*	20	5	5	13	13	10
Austroperla cyrene	*sh*	1	0	0	0	0	3
Stenaperla maclellani	*p*	0	0	0	0	1	0
Taraperla howsei	*cb*	1	0	0	0	0	10
Zelandoperla sp.	*cb*	0	0	0	3	11	10
Zelandobius unicolor	*cb*	0	0	0	0	0	1
Zelandobius pilosus	*cb*	1	1	1	0	0	1
Zelandobius confusus	*cb*	0	0	0	0	0	0
Zelandobius furcillatus	*cb*	1	1	0	0	1	1
Cristaperla sp.	*cb*	0	0	0	0	0	0
Spaniocerca sp.	*cb*	1	1	0	0	0	1
Megaleptoperla grandis	*p*	0	0	0	1	0	0
Halticoperla viridans	*cb*	0	1	0	0	0	0
Aoteapsyche colonica	*f*	0	0	0	0	0	0
Beraeoptera roria	*cb*	0	0	1	0	1	0
Oxyethira sp.	*hp*	1	1	3	0	1	0
Paroxyethira eatoni	*hp*	0	0	0	0	0	0
Psilochorema sp.	*p*	5	1	3	5	1	0
Olinga feredayi	*cb*	0	0	0	0	0	3
Hydrobiosidae indent.	*p*	1	0	0	0	0	1
Hydrobiosis charadraea	*p*	0	0	0	0	0	0
Hydrobiosis clavigera	*p*	0	0	0	0	0	0
Hydrobiosis parumbripennis	*p*	5	5	3	1	0	0

Hydrobiosis torrentis	*p*	0	0	0	0	0	0
Hydrobiosis soro	*p*	0	0	0	0	0	0
Hydrobiosis neadelphus (styx)	*p*	0	0	0	0	0	0
Hydrobiosis silvicola-gp	*p*	0	0	0	0	0	0
Hydrobiosis chalcodes	*p*	1	0	1	0	0	0
Hydrobiosis harpidiosa	*p*	0	0	0	0	0	0
Costachorema xanthopterum	*p*	0	0	0	0	0	0
Polyplectropus sp.	*p*	0	0	0	0	0	0
Philorheithrus agilis	*p*	1	0	0	0	0	0
Oeconesus sp.	*cb*	1	1	0	0	0	0
Hudsonema amabile	*p*	0	0	0	0	0	0
Hudsonema alienium	*p*	1	0	0	0	0	0
Triplectides obsoletus	*sh*	0	0	0	0	0	0
Pycnocentrodes sp.	*cb*	5	5	3	5	0	0
Pycnocentria funerea	*cb*	0	0	0	0	0	0
Pycnocentria evecta	*cb*	0	0	0	0	0	0
Edpercivalia sp.	*p*	0	0	0	0	0	0
Hydrobiosella sp.	*f*	0	0	0	0	0	0
Hydrochorema tenuicaudatum	*p*	0	0	0	0	0	0
Trailochorema	p	0	0	0	0	0	0
Costachorema psaropterum	*p*	0	0	0	0	0	1
Pycnocentria sylvestris	*cb*	0	0	0	0	0	0
Zealandopsyche ingens	*sh*	0	0	0	0	0	0
Ocetis unicolor	*p*	0	0	0	0	0	0
Zellolisica cheira	*cb*	0	0	0	0	0	0
Scirtidae	*cb*	1	1	3	1	0	0
Huxelhydrus syntheticus	*p*	0	0	0	0	0	0
Antiporus stigosulus	*p*	0	0	0	0	0	0
Liodessus deflectus	*p*	0	0	0	0	0	0
Hydrophilidae	*p*	0	0	0	0	0	0
Antiporus femoralis	p	0	0	0	0	0	0
Ptilodactylidae	*cb*	0	0	0	0	0	0
Hydraenidae	*sh*	0	0	0	0	0	1
Elmidae	*cb*	0	0	0	3	3	10
Hexatomini sp.	*cb*	0	0	0	1	0	0
Psychodidae	*cb*	0	0	0	0	0	0
Ceratopogonidae	*p*	0	0	0	0	0	0
Sciomyzidae	*p*	0	0	0	0	0	0
Limonia sp.	*sh*	1	1	3	3	0	0
Muscidae	*cb*	1	1	3	1	0	1
Aphrophila sp.	*cb*	0	0	0	5	0	1
Zelandotipula sp.	*cb*	0	0	0	0	0	0
Tabanidae	*p*	0	0	0	0	0	0
Eriopterini	*cb*	0	0	0	3	0	0
Neocurupira	*sc*	0	0	0	0	3	3
Stradiomyidae	*cb*	0	0	0	0	0	0
Empididae	*cb*	0	0	0	0	0	0
culex	*f*	0	0	0	0	0	0
Nothodixa	*cb*	0	1	0	0	0	0
Austrosimulium	*f*	0	1	0	3	3	3
Tanypodinae	*p*	0	1	0	1	3	3
Chironominae	*cb*	0	1	0	0	0	0
Diamesinae	*cb*	20	1	11	1	0	3
Orthocladiinae	*cb*	100	1	20	5	13	3

Potamopyrgus antipodarum	*sc*	20	20	0	0	0	0
Sphaeriadae	*f*	0	0	0	0	0	0
Lymnae tomentosa	*sc*	0	0	0	0	0	0
Phreatogammerus sp.	*cb*	0	0	0	0	0	0
Paraleptamphopus sp.	*cb*	20	1	3	3	0	0
Ostracod	*f*	0	0	0	0	0	0
Turbellaria	*p*	5	1	0	0	0	1
Prorhynchus putealis	*p*	1	0	0	0	0	0
Hirudinae	*p*	0	0	0	0	0	0
Acari	*p*	1	1	0	0	0	0
Oniscoidea	*cb*	0	0	0	0	0	0
Oligochaeta	*cb*	0	3	0	0	0	0
Nematomorpha		0	0	0	0	0	1
Archicauliodes diversus	*p*	0	0	0	0	0	0
Sigara sp.	hp	0	0	0	0	0	0